SYSTEMATIC IMPLICATIONS OF POLLEN MORPHOLOGY IN SUBFAMILIES LAMIOIDEAE AND POGOSTEMONOIDEAE (LABIATAE)[1]

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ABSTRACT

Pollen morphology was surveyed in 57 of the 60 genera of Lamioideae and Pogostemonoideae sensu Cantino et al. and two genera of uncertain subfamilial affinities: *Anisomeles* and *Eurysolen*. Pollen in all Pogostemonoideae, most Lamioideae, *Anisomeles*, and *Eurysolen* is tricolpate with suprareticulate sculpturing. Variants found in a few genera of Lamioideae include tetracolpate and hexapantocolpate pollen and psilate, granulate, and rugulate sculpturing. Most species in which pollen was examined in section have simple columellae, but seemingly branched columellae were observed in *Gomphostemma*, *Chelonopsis*, and one species of *Stenogyne*. With regard to the genera of uncertain affinities, the findings presented here support a relationship between *Anisomeles* and *Pogostemon*; the position of *Eurysolen* remains unclear. Within subfamily Lamioideae, pollen morphology supports the segregation of *Lamiophlomis*, *Lagopsis*, and *Phlomidoschema* from *Phlomis*, *Marrubium*, and *Stachys*, respectively. Hexapantocolpate pollen is hypothesized to be a synapomorphy of *Sideritis* section *Empedoclea*. Similarities in pollen sculpturing were noted between *Brazoria*, *Macbridea*, and *Physostegia*, and between *Galeopsis* and *Synandra*.

A pollen survey of subfamily Lamioideae sensu Erdtman (1945) was undertaken with the hope that it might further our understanding of systematic relationships. A brief overview of the study as a whole has been published (Abu-Asab & Cantino, 1992), with elaboration elsewhere on two small subgroups that appear not to be closely related to the remainder of the study group (Abu-Asab & Cantino, 1993a, b). It is our intent here to document in detail the pollen morphology of the bulk of Erdtman's Lamioideae—i.e., those genera with a gynobasic style.

A taxonomic clarification is needed because we have circumscribed subfamily Lamioideae differently here than in some of our earlier works (e.g., Cantino & Sanders, 1986; Abu-Asab, 1990; Cantino, 1990, 1992a; Abu-Asab & Cantino, 1992). Although the pollen survey was initiated as a study of the Lamioideae sensu Erdtman (1945), and our earlier papers adopted Erdtman's circumscription, recent evidence that this taxon is polyphyletic (Abu-Asab & Cantino, 1992; Cantino, 1992b) led to an alternative classification (Cantino et al., 1992), which is followed here. Unless otherwise indicated, all references herein to subfamily Lamioideae imply the circumscription of Cantino et al. (1992).

Subfamily Lamioideae comprises 55 genera, the vast majority of them Eurasian (Table 1). Subfamily Pogostemonoideae is an Asian group of five genera. Based on morphological and molecular evidence, the two subfamilies are closely related (Cantino, 1992a; Downie & Palmer, 1992), and *Eurysolen* resembles genera in both. (See Table 1 for authors of genus names and Appendix for authors of species names.) *Anisomeles* has been variably assigned to both subfamilies (see Discussion).

Most pollen studies that included members of Lamioideae and Pogostemonoideae have centered on particular genera (e.g., Huynh, 1972; Bassett & Munro, 1986) or geographical regions (e.g., Waterman, 1960; Varghese & Verma, 1968; Huang, 1972). Risch (1956) and Pozhidaev (1989) conducted broader surveys of the Labiatae, but Risch used only light microscopy, and his descrip-

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TABLE 1. Genera of Lamioideae and Pogostemonoideae. Numbers in parentheses: number of species in the genus/number of species studied (Appendix). Numbers of species were taken from a variety of sources, geographic distributions mostly from Mabberley (1987) and Airy Shaw (1973).

Subfamily Lamioideae

Achyrospermum Blume (10/6)—Paleotropics
Acrotome Benth. ex Endl. (8/4)—Tropical & southern Africa
Ajugoides Makino (1/1)—Japan
Alajja Ikonn. (1/1)—Himalayas
Ballota L. (35/7)—Europe, Africa, western Asia
Bostrychanthera Benth. (1/0)—China
Brazoria Engelm. & A. Gray (4/4)—Texas, Oklahoma
Chaiturus Willd. (1/1)—Temperate Eurasia
Chamaesphacos Schrenk ex Fischer & C Meyer (1/1)—Central & southwestern Asia
Chelonopsis Miq. (13/2)—Himalayas, China, Japan
Colquhounia Wallich (5/2)—Himalayas
Craniotome Rchb. (1/1)—Himalayas
Eremostachys Bunge ex Ledeb. sensu lato (60/4)—Europe to central Asia
Eriophyton Benth. (1/1)—Himalayas
Galeopsis L. (10/6)—Temperate Eurasia
Gomphostemma Wallich ex Benth. (30/7)—Southeastern Asia, Malesia
Haplostachys (A. Gray) Hillebrand (5/2)—Hawaii
Hypogomphia Bunge (1/1)—Central & southwestern Asia
Isoleucas Schwartz (1/0)—Arabia
Lagochilus Bunge ex Benth. (35/3)—Central & southwestern Asia
Lagopsis Bunge (4/2)—Western Siberia to Japan
Lamiophlomis Kudo (1/1)—Himalayas
Lamium L. (16/7)—Temperate Eurasia, northern Africa
Leonotis (Pers.) R. Br. (15/3)—Tropical & southern Africa, 1 pantropical
Leonurus L. (24/2)—Temperate Eurasia
Leucas R. Br. (100/17)—Pantropical, southern Africa, China
Loxocalyx Hemsley (3/2)—China, Japan
Macbridea Elliott ex Nutt. (2/2)—Southeastern United States
Marrubium L. (30/5)—Europe, northern Africa, central & southwestern Asia
Melittis L. (1/1)—Europe
Metastachydium Airy Shaw ex C. Y. Wu & Li (1/1)—Central Asia
Microtoena Prain (25/4)—Himalayas, China
Moluccella L. (2/2)—Southern Europe, southwestern Asia
Notochaete Benth. (1/1)—Himalayas
Otostegia Benth. (20/5)—Northeastern tropical Africa to central Asia
Panzerina Soják (2/1)—Western Siberia to Mongolia
Paralamium Dunn (1/1)—Southwestern China

TABLE 1. Continued.

Paraphlomis Prain (8/3)—Eastern Asia, Malesia
Phlomidoschema (Benth.) Vved. (1/1)—Iran to western Himalayas
Phlomis L. (ca. 100/7)—Mediterranean region to China
Phyllostegia Benth. (28/5)—Hawaii, Tahiti
Physostegia Benth. (12/2)—North America
Prasium L. (1/1)—Mediterranean region
Pseuderemostachys Popov (1/1)—Central Asia
Pseudomarrubium Popov (1/0)—Central Asia
Roylea Wallich ex Benth. (1/1)—Himalayas
Sideritis L. (ca. 130/19)—Mediterranean region to southwestern Asia, Macaronesia
Stachyopsis Popov & Vved. (3/1)—Central Asia to western China
Stachys L. (ca. 300/2)—Northern & southern temperate & subtropical; tropical mountains
Stenogyne Benth. (20/3)—Hawaii
Sulaimania Hedge & Rech. f. (1/1)—Pakistan
Suzukia Kudo (2/1)—Taiwan, Ryukyus
Synandra Nutt. (1/1)—Eastern United States
Thuspeinanta T. Durand (2/1)—Central & southwestern Asia
Weidemannia Fischer & C. Meyer (2/1)—Southwestern Asia

Subfamily Pogostemonoideae

Colebrookea Smith (1/1)—India
Comanthosphace S. Moore (7/3)—Eastern Asia
Leucosceptrum Smith (1/1)—Himalayas, China
Pogostemon Desf. (71/10)—China, India, Malesia
Rostrinucula Kudo (2/1)—Eastern Asia

Genera of uncertain affinities

Anisomeles R. Br. (6/4)—Paleotropics
Eurysolen Prain (1/1)—Southeastern Asia, Indomalesia

tions emphasized gross pollen morphology (i.e., size, shape, color). Pozhidaev's (1989) survey used scanning electron microscopy (SEM), but the resulting publication focused on variation in exine structure in the family as a whole; the pollen morphology of individual genera was not systematically described, and micrographs were provided for less than a third of the genera studied. We are aware of published SEM pollen micrographs for only 25 of the 60 genera of Lamioideae and Pogostemonoideae (Nabli, 1976; Roca Salinas, 1978; Azizian & Moore, 1982; Cantino, 1982; Ubera & Galán, 1983; Bassett & Munro, 1986; Cantino & Sanders, 1986; Pozhidaev, 1989, 1992; Abu-Asab & Cantino, 1992; Demissew & Harley, 1992; Trudel & Morton, 1992). Few species have been studied, so the degree of intrageneric variation in surface sculpturing is unknown for most of these genera;

exceptions are *Eremostachys*, *Paraphlomis*, *Phlomis*, *Physostegia*, and *Stachys*. Transmission electron microscope (TEM) photographs have been published for only three genera (Nabli, 1976; Abu-Asab & Cantino, 1992).

The objectives of this paper are to document the pollen morphology of subfamilies Lamioideae and Pogostemonoideae, including interspecific variation within most of the larger genera, and to evaluate the systematic significance of the resulting data. Because the resulting compilation of SEM photographs includes nearly every genus in these subfamilies, it should serve as a useful reference for those studying the systematics or palynology of the Labiatae.

Materials and Methods

The study collection (Table 1) comprised 183 species representing all five genera of Pogostemonoideae, 52 of the 55 genera of Lamioideae, and two genera of uncertain subfamilial affinities (*Anisomeles* and *Eurysolen*). In most of the larger genera, an effort was made to sample a broad spectrum of species by reference to the infrageneric classifications of Briquet (1895–1897) and available monographs and revisions. *Eremostachys*, *Phlomis*, *Physostegia*, and *Stachys* were only superficially sampled because they have already received considerable study (Azizian & Moore, 1982; Cantino, 1982; Ubera & Galán, 1983; Bassett & Munro, 1986; Demissew & Harley, 1992). The monotypic genera *Bostrychanthera*, *Pseudomarrubium*, and *Isoleucas* were not examined for lack of material, but micrographs of the former two were provided by Pozhidaev (1989); thus only the pollen of *Isoleucas* remains totally unknown.

Pollen obtained from mature buds (vouchers listed in Appendix) was prepared for SEM, TEM, and light microscopy (LM) using the prolonged acetolysis procedure of Abu-Asab & Cantino (1989), modified from Erdtman (1960). For LM, including size measurements, the pollen was mounted in glycerine jelly and sealed with paraffin. In most cases, seven to ten grains were measured per species. The ratio of polar to equatorial axis length (P/E) was determined for each measured grain, and the mean P/E ratio was calculated from these individual values. For SEM, pollen was coated with gold-palladium and examined and photographed with a Hitachi HHS-2R scanning electron microscope. For TEM, pollen was treated with osmium tetroxide, stained with uranyl acetate, and embedded in resin. Thin sections were collected on carbon-stabilized Formvar, stained with aqueous uranyl acetate and lead citrate, and examined and photographed with a Hitachi HS-8 transmission electron microscope.

Results

The results are summarized in Table 2, and representative pollen grains are illustrated in Figures 1–247. The distinction between foveolate, microreticulate, punctate, reticulate, and scrobiculate sculpturing follows Vezey et al. (1992), a more precise system of terminology than used in our previous papers (Abu-Asab, 1990; Abu-Asab & Cantino, 1989, 1992, 1993a, b; Abu-Asab et al., 1993). Pollen that we previously referred to as tectate-perforate is described here as scrobiculate or punctate.

LAMIOIDEAE

Pollen of subfamily Lamioideae is suboblate to euprolate (shape classification follows Walker & Doyle, 1975, based on P/E ratios in Table 2), with the polar axis 15–59 μm and the equatorial axis 13–52 μm. The grains are inoperculate and usually tricolpate; tetracolpate and hexapantocolpate grains were found in a few genera (Table 2). The exine in most species is scrobiculate (sometimes bordering on microreticulate or punctate). The exine is microreticulate in seven species, reticulate in one, and partially foveolate in one (Table 2). The sculpturing is suprareticulate in most species (referred to as bi-reticulate by some authors; Demissew & Harley, 1992; Harley et al., 1992), but four other forms of sculpturing were found: psilate, granulate, rugulate, and suprareticulate-rugulate. The columellae are usually simple but sparsely branched in a few species.

The pollen features in a few genera warrant a more detailed description than is available in Table 2:

Gomphostemma (Figs. 62–76; Pozhidaev, 1989): sculpturing exceptionally variable: psilate or with suprareticulate, rugulate, or granulate sculpturing; columellae branched.

Lagopsis (Fig. 77): exine rugulate, psilate toward the poles, apparently nonperforate.

Sideritis (Figs. 182–196; Huynh, 1972; Nabli, 1976; Roca Salinas, 1978; Pozhidaev, 1992): tetracolpate (the amb circular to more or less square), 6-pantocolpate (the amb circular), or rarely tricolpate (the amb triangular); exine psilate (approaching a suprareticulate condition in section *Empedoclea* (Raf.) Benth.; Figs. 192, 193), usually scrobiculate (in *S. montana*, the polar regions and centers of the three mesocolpia foveolate, the

TABLE 2. Summary of pollen morphological data for subfamilies Lamioideae and Pogostemonoideae and genera of uncertain affinities. Colpi: 3, tricolpate; 4, tetracolpate; 6, hexapantocolpate. Columellae: simple vs. branched. Sculpturing: Upper layer: Gr, granulate; Ps, psilate; Ru, rugulate; Sr, suprareticulate-rugulate; Su, suprareticulate. Lower layer (or only layer if psilate): Fo, foveolate; Mi, microreticulate; Np, nonperforate; Pu, punctate; Re, reticulate; Sc, scrobiculate; slash indicates borderline designations.

	Polar axis (μm)		Equatorial axis (μm)		P/E ratio				Sculpturing		
Species	Mean	Range	Mean	Range	Mean	Range	Colpi	Columellae	Upper	Lower	Figures
Subfamily Lamioideae											
Achyrospermum aethiopicum	21.3	(20–22)	18.5	(18–20)	1.16	(1.0–1.3)	3		Su	Sc	1, 2
Achyrospermum carvalhi	26.9	(22–31)	23.9	(20–29)	1.13	(0.8–1.3)	3		Su	Sc/Mi	3
Achyrospermum cryptanthum	24.0	(22–31)	19.1	(18–22)	1.25	(1.1–1.4)	3		Su	Sc	4
Achyrospermum densiflorum	24.5	(22–26)	18.4	(15–22)	1.34	(1.0–1.7)	3		Su	Sc	5
Achyrospermum parviflorum	23.3	(22–24)	18.9	(18–20)	1.24	(1.1–1.3)	3		Su	Sc	6, 7
Achyrospermum schimperi	28.0	(22–33)	20.9	(20–22)	1.34	(1.1–1.5)	3		Su	Sc	8, 9
Acrotome angustifolia	20.2	(20–22)	18.0	(17–20)	1.13	(1.0–1.3)	3		Su	Sc	10, 11
Acrotome fleckii	20.7	(20–22)	22.0	(20–24)	0.94	(0.8–1.1)	3		?	?	
Acrotome hispida	20.0	(—)	21.6	(20–22)	0.92	(0.9–1.0)	3		?	?	
Acrotome inflata	22.9	(22–24)	22.9	(22–24)	1.00	(0.9–1.1)	3		?	?	
Ajugoides humilis	31.9	(31–35)	23.5	(22–26)	1.36	(1.2–1.6)	3		Su	Sc/Mi	12, 13
Alajja rhomboidea	30.1	(29–33)	28.4	(26–31)	1.06	(0.9–1.3)	3		Su	Sc	14, 15
Ballota africana	22.7	(22–24)	20.7	(20–22)	1.10	(1.0–1.2)	3		Su	Sc	16
Ballota andreuzziana	23.5	(22–24)	20.9	(20–22)	1.13	(1.0–1.2)	3		Su	Sc/Mi	
Ballota hirsuta	22.0	(—)	18.0	(17–20)	1.22	(1.1–1.3)	3		Su	Sc	17, 18
Ballota integrifolia	21.6	(20–24)	21.3	(20–24)	1.01	(0.9–1.1)	3		Su	Mi	19
Ballota nigra	23.8	(22–26)	20.9	(18–24)	1.14	(1.0–1.3)	3		Su	Sc	20
Ballota pseudodictamnus	29.3	(26–31)	20.5	(18–22)	1.43	(1.3–1.6)	3		Su	Sc/Mi	21, 22
Ballota rupestris	21.2	(20–22)	23.4	(22–24)	0.90	(—)	3		Su	Sc	
Brazoria arenaria	35.2	(33–40)	32.3	(31–33)	1.09	(1.0–1.2)	3		Su	Sc	23
Brazoria pulcherrima	37.0	(35–42)	31.7	(29–33)	1.17	(1.1–1.5)	3		Su	Sc	24
Brazoria scutellarioides	32.5	(29–35)	33.0	(29–35)	0.99	(0.8–1.2)	3		Su	?	25
Brazoria truncata	39.2	(37–42)	32.6	(29–35)	1.21	(1.1–1.5)	3		Su	Sc	26, 27
Chaiturus marrubiastrum	21.2	(20–23)	20.5	(18–22)	1.04	(0.9–1.2)	3		Su	Sc	28, 29
Chamaesphacos ilicifolius	30.4	(24–33)	24.0	(20–26)	1.27	(1.1–1.4)	3		Su	Sc	30
Chelonopsis lichiangensis	28.4	(24–31)	27.3	(24–31)	1.04	(0.9–1.2)	3	Branched?	Su	Sc/Mi	31, 32
Chelonopsis odontochila	28.0	(26–29)	26.4	(24–29)	1.06	(1.0–1.2)	3		Su	Sc/Mi	33, 34
Colquhounia coccinea	27.7	(26–31)	26.6	(26–29)	1.04	(0.9–1.2)	3		Su	Sc	
Colquhounia seguinii	23.3	(22–26)	21.6	(20–24)	1.09	(0.9–1.3)	3		Su	Sc	35, 36
Craniotome furcata	16.6	(15–18)	14.9	(13–15)	1.12	(1.0–1.3)	3		Su	Sc	37–39
Eremostachys fetissovii	33.4	(31–37)	29.5	(24–33)	1.14	(0.9–1.6)	3		Su	Sc	
Eremostachys iliensis	31.7	(31–33)	27.1	(24–29)	1.17	(1.1–1.3)	3		Su	Sc	40, 41

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Eremostachys rotata	34.5	(29–37)	32.3	(29–35)	1.07	(0.8–1.2)	3		Su	Sc	42
Eremostachys speciosa	35.9	(33–37)	29.5	(26–33)	1.23	(1.1–1.4)	3		Su	Sc	43
Eriophyton wallichianum	28.6	(26–31)	23.5	(22–26)	1.22	(1.0–1.4)	3		Su	Sc	44, 45
Galeopsis bifida	38.7	(33–46)	32.1	(26–37)	1.22	(0.9–1.4)	3		Su	Sc	46, 47
Galeopsis ladanum	34.9	(31–40)	26.7	(24–31)	1.31	(1.2–1.5)	3		Su	Sc	
Galeopsis pubescens	32.1	(26–35)	26.0	(22–31)	1.24	(1.0–1.4)	3		Su	Sc	48
Galeopsis segetum	35.2	(31–40)	26.8	(24–31)	1.32	(1.0–1.6)	3		Su	?	
Galeopsis speciosa	37.8	(35–40)	27.3	(26–29)	1.39	(1.2–1.5)	3		Su	Sc	49
Galeopsis tetrahit	38.5	(35–42)	29.0	(26–31)	1.33	(1.1–1.5)	3		Su	Sc	50
Gomphostemma chinense	33.7	(31–35)	33.4	(33–35)	1.01	(0.9–1.1)	3		Gr	Sc/Mi	62, 63
Gomphostemma intermedium	32.1	(31–35)	32.6	(31–33)	0.99	(0.9–1.0)	3	Branched	Ps	Mi	64–66
Gomphostemma javanicum	29.7	(26–31)	30.8	(29–33)	0.97	(0.9–1.0)	3		Ru	Sc	69, 70
Gomphostemma leptodon	33.2	(29–40)	35.4	(29–42)	0.94	(0.9–1.2)	3		Ps	Sc	67, 68
Gomphostemma lucidum	32.3	(29–37)	32.6	(31–33)	0.99	(0.8–1.1)	3	Branched	Ps	Sc	71, 72
Gomphostemma parviflorum	26.6	(24–29)	25.7	(24–29)	1.04	(0.9–1.1)	3		Gr	Sc	73, 74
Gomphostemma wallichii	29.9	(29–31)	31.7	(31–33)	0.95	(0.9–1.0)	3		Su	Sc	75, 76
Haplostachys haplostachya	51.0	(44–57)	48.4	(46–51)	1.06	(0.9–1.2)	3, 4		Su	Sc	51, 52
Haplostachys linearifolia	49.7	(46–55)	46.2	(44–48)	1.08	(1.0–1.2)	3, 4		Su	Sc	53, 54
Hypogomphia turkestana	33.4	(29–40)	27.4	(24–29)	1.22	(1.0–1.5)	3	Simple	Su	Sc	55–57
Lagochilus aucheri	25.5	(24–26)	24.2	(22–26)	1.06	(1.0–1.2)	3		Su	?	58, 59
Lagochilus diacanthophyllus	28.2	(26–29)	22.7	(20–24)	1.25	(1.1–1.4)	3		Su	Sc	60, 61
Lagochilus hirtus	25.5	(22–29)	21.1	(20–24)	1.22	(0.9–1.3)	3		Su	Sc	
Lagopsis marrubiastrum	21.2	(20–23)	19.6	(18–21)	1.08	(0.9–1.2)	3		Ru+Ps	Np?	77
Lagopsis supina	21.1	(20–22)	21.8	(20–24)	0.97	(0.9–1.1)	3		?	?	
Lamiophlomis rotata	24.2	(22–26)	20.0	(18–22)	1.21	(1.1–1.3)	3		Ps	Sc	78, 79
Lamium album	25.1	(22–29)	23.8	(22–26)	1.06	(0.8–1.3)	3		Gr	Sc	80, 81
Lamium flexuosum	23.5	(22–26)	21.8	(18–24)	1.09	(0.9–1.3)	3	Simple	Su	Sc	82, 83
Lamium galeobdolon	30.8	(29–33)	22.9	(20–26)	1.36	(1.1–1.6)	3		Su	Sc	86, 87
Lamium garganicum	28.6	(26–33)	26.8	(24–29)	1.07	(1.0–1.2)	3	Simple	Su	Mi	84, 85
Lamium moluccellifolium	34.1	(33–35)	30.1	(26–33)	1.14	(1.0–1.3)	3		Su	?	
Lamium moschatum	21.2	(20–22)	20.6	(20–22)	1.03	(0.9–1.1)	3		Gr	Sc	88, 89
Lamium purpureum							3		Su	Sc	90, 91
Leonotis bequaertii	30.7	(29–33)	29.9	(28–33)	1.02	(0.8–1.2)	3		Su	Sc	92, 93
Leonotis leonitis	28.6	(26–31)	24.9	(24–26)	1.15	(1.1–1.3)	3	Simple	Su	Sc	94–96
Leonotis mollissima	31.9	(29–35)	28.6	(22–33)	1.13	(0.9–1.5)	3	Simple	Su	Sc	97

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Leonurus cardiaca	22.7	(22–24)	21.1	(20–24)	1.08	(1.0–1.1)	3		Su	Sc	98, 99
Leonurus sibiricus	25.5	(22–29)	21.3	(20–24)	1.20	(1.0–1.4)	3		Su	Sc	100
Leucas abyssinica	20.5	(18–22)	19.1	(18–20)	1.07	(1.0–1.1)	3		Su	Sc	107, 108
Leucas alluaudii	26.0	(22–31)	22.9	(20–26)	1.14	(1.0–1.4)	3		Su	Sc	109
Leucas aspera	24.0	(22–26)	19.6	(18–22)	1.23	(1.1–1.4)	3		Su	Sc/Mi	110, 111
Leucas biflora	29.3	(26–31)	23.1	(22–26)	1.27	(1.1–1.4)	3		Su	Sc	
Leucas calostachys	25.3	(24–26)	22.4	(20–24)	1.14	(1.0–1.3)	3		Su	Sc	112, 113
Leucas ciliata	23.3	(22–24)	22.7	(22–24)	1.03	(0.9–1.1)	3		Su	Sc	
Leucas eriostoma	20.9	(20–22)	17.6	(15–20)	1.20	(1.1–1.4)	3		Su	Mi	114
Leucas hirta	20.5	(20–22)	16.7	(15–20)	1.24	(1.0–1.4)	3		Su	Sc	115
Leucas inflata	20.0	(—)	18.1	(17–20)	1.10	(1.0–1.1)	3		Su?	?	116
Leucas javanica	26.4	(22–31)	24.2	(22–26)	1.09	(0.9–1.3)	3		Su	Sc/Mi	117
Leucas lanata	27.3	(26–29)	20.5	(18–22)	1.34	(1.2–1.5)	3		Su	Sc	
Leucas lavandulifolia	26.4	(24–29)	22.7	(20–24)	1.17	(1.1–1.3)	3		Su	Sc	
Leucas marrubioides	22.9	(20–24)	17.8	(15–20)	1.29	(1.0–1.4)	3		?	?	
Leucas martinicensis	22.6	(22–24)	20.1	(19–22)	1.13	(1.0–1.2)	3		Su	Sc	
Leucas mollissima	29.6	(29–31)	23.0	(22–24)	1.29	(1.2–1.4)	3		?	?	
Leucas rosmarinifolia	22.2	(20–24)	18.5	(18–20)	1.21	(1.1–1.4)	3	Simple	Su	?	118
Leucas stelligera	21.1	(20–24)	18.9	(18–20)	1.12	(1.0–1.3)	3		Su	Sc	
Loxocalyx ambiguus	23.8	(22–26)	21.3	(20–22)	1.12	(1.0–1.3)	3		Su	Sc/Mi	101
Loxocalyx urticifolius	24.0	(22–26)	20.9	(20–24)	1.16	(0.9–1.3)	3		Su	Sc	102, 103
Macbridea alba	47.3	(42–53)	34.5	(31–37)	1.37	(1.2–1.5)	3		Su	Sc	104
Macbridea caroliniana	38.1	(35–42)	40.5	(40–42)	0.94	(0.9–1.1)	3		Su	Sc	105, 106
Marrubium anisodon	27.5	(24–31)	29.0	(26–31)	0.95	(0.8–1.1)	4		Ps	Sc	122, 123
Marrubium cuneatum	24.9	(24–26)	26.8	(24–29)	0.93	(0.8–1.1)	3		Ps	Sc	
Marrubium heterodon	26.4	(24–29)	27.7	(26–29)	0.95	(0.8–1.1)	3		Ps	Sc/Pu	124, 125
Marrubium incanum	52.3	(51–55)	46.9	(44–51)	1.12	(1.1–1.2)	3		Ps	Sc/Pu	
Marrubium supinum	24.0	(—)	25.9	(24–26)	0.93	(0.9–1.0)	3	Simple	Ps	Sc	126–128
Melittis melissophyllum	45.8	(40–51)	35.6	(31–40)	1.29	(1.2–1.5)	3		Su	Sc	119, 120
Metastachydium sagittatum	22.2	(22–24)	23.1	(22–24)	0.96	(0.9–1.1)	3		Su	Sc	121
Microtoena delavayi							3	Simple	Su	Sc/Mi	129–131
Microtoena insuavis							3		Su	Mi	132
Microtoena robusta	32.8	(29–37)	28.8	(24–33)	1.15	(0.9–1.4)	3		Su	Mi	133, 134
Microtoena urticifolia	24.6	(22–26)	28.2	(24–31)	0.88	(0.8–0.9)	3		Su	Mi	135, 136
Moluccella laevis	34.8	(33–40)	28.2	(26–31)	1.24	(1.1–1.5)	3		Su	Sc/Mi	137

TABLE 2. Continued.

Species	Polar axis (µm)		Equatorial axis (µm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Moluccella spinosa	29.5	(29–31)	30.4	(29–31)	0.97	(0.9–1.1)	3		Su	Sc	138, 139
Notochaete hamosa	30.1	(26–33)	29.3	(26–31)	1.03	(0.8–1.2)	3		Ps	Sc	140, 141
Otostegia fruticosa	21.8	(20–22)	21	(20–22)	1.04	(1.0–1.1)	3		Su	Sc	142, 143
Otostegia integrifolia	29.0	(26–33)	23.8	(22–26)	1.23	(1.0–1.4)	3		Su	Sc/Mi	144
Otostegia minuccii	24.2	(22–26)	21.1	(20–22)	1.15	(1.0–1.2)	3		Su	Sc	
Otostegia repanda	20.9	(20–22)	17.2	(15–18)	1.22	(1.1–1.4)	3		Su	Sc	145
Otostegia tomentosa	21.1	(18–22)	18.3	(18–20)	1.16	(1.0–1.3)	3	Simple	Su	Sc	146, 147
Panzerina lanata	23.3	(22–26)	19.4	(18–22)	1.21	(1.0–1.5)	3		Su	Sc	148–150
Paralamium gracile	16.3	(15–20)	15.0	(13–18)	1.10	(0.9–1.5)	3		Su	Sc	151
Paraphlomis javanica	30.1	(29–33)	32.8	(29–35)	0.92	(0.8–1.0)	3		Sr	Sc	152, 153
Paraphlomis lanceolata	26.8	(26–29)	26.0	(24–29)	1.04	(1.0–1.2)	3		Su	Sc/Mi	154, 155
Paraphlomis rugosa	30.0	(26–37)	31.2	(29–37)	0.96	(0.8–1.1)	3		Su	Sc	156
Phlomidoschema parviflorum	24.2	(22–26)	21.6	(18–26)	1.14	(1.0–1.4)	3		Ps	Sc	157, 158
Phlomis agraria	29.5	(29–31)	25.7	(24–29)	1.15	(1.0–1.3)	3		Su	Sc	159, 160
Phlomis crinita	33.9	(33–35)	25.1	(22–26)	1.36	(1.3–1.5)	3		Su	?	
Phlomis herba-venti	34.1	(31–37)	28.4	(26–31)	1.20	(1.1–1.4)	3		?	?	
Phlomis lanata	40.3	(37–44)	29.0	(26–33)	1.39	(1.2–1.6)	3		Su	Sc	161, 162
Phlomis maximoviczii	20.9	(20–22)	18.9	(18–20)	1.11	(1.0–1.3)	3		Gr	Sc	163
Phlomis tuberosa	27.3	(24–29)	25.5	(24–26)	1.07	(1.0–1.2)	3		Su	Sc	164
Phlomis umbrosa	19.6	(18–22)	16.1	(15–18)	1.22	(1.1–1.3)	3		Gr	Sc/Mi	165, 166
Phyllostegia grandiflora	42.5	(40–44)	45.8	(44–48)	0.93	(0.8–1.0)	3		Ps	Re	167, 168
Phyllostegia hirsuta	39.8	(37–44)	41.1	(35–46)	0.97	(0.9–1.1)	3		Su	Sc	169, 170
Phyllostegia hispida	35	(33–37)	36.3	(35–37)	0.96	(0.9–1.1)	3		Su	Sc	171, 172
Phyllostegia lantanoides	36.3	(35–37)	38.1	(37–40)	0.95	(0.9–1.0)	3		Su	Sc	173
Phyllostegia racemosa	33.2	(33–35)	36.1	(33–37)	0.92	(0.8–1.0)	3		Su	Sc	174
Physostegia longisepala	55.9	(53–59)	48.4	(46–52)	1.16	(1.1–1.3)	3		Su	Sc	175, 176
Physostegia pulchella	45.8	(43–48)	42.3	(36–46)	1.09	(1.0–1.3)	3		Su	Sc	
Prasium majus	35.9	(33–40)	30.6	(26–44)	1.19	(0.9–1.4)	3		Su	Sc	177

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Pseuderemostachys sewertzowii	37.0	(31–42)	29.0	(26–31)	1.28	(1.0–1.5)	3		Su	Sc	178, 179
Roylea cinerea	22.2	(20–24)	22.0	(20–24)	1.02	(0.8–1.2)	3		Su	Sc/Mi	180, 181
Sideritis canariensis	31.7	(31–33)	35.0	(33–37)	0.91	(0.8–1.0)	4		Ps	Sc	182, 183
Sideritis candicans	44.0	(42–46)	40.3	(35–44)	1.10	(1.0–1.3)	4		Ps	Sc	184
Sideritis chlorostegia	30.4	(29–33)	30.4	(29–33)	1.00	(—)	6		Ps	Sc	191, 192
Sideritis curvidens	26.6	(24–29)	22.2	(20–24)	1.20	(1.1–1.3)	4		Ps	Sc	185
Sideritis euboea	31.7	(29–33)	31.7	(29–33)	1.00	(—)	6		Ps	Sc	193
Sideritis gomerae	36.3	(35–40)	33.9	(31–37)	1.08	(0.9–1.2)	4		Ps	Sc	
Sideritis hirsuta	31.9	(31–33)	29.7	(26–33)	1.08	(1.0–1.2)	4		Ps	Sc	
Sideritis hololeuca	31.5	(29–33)	31.5	(29–33)	1.00	(—)	6		Ps	Sc	194
Sideritis hyssopifolia	27.5	(24–31)	25.5	(22–29)	1.09	(0.9–1.4)	4		Ps	Sc	186
Sideritis ilicifolia	32.8	(31–35)	24.9	(22–29)	1.33	(1.2–1.5)	4		Ps	Sc/Pu	187
Sideritis incana	26.2	(24–29)	24.6	(24–26)	1.06	(1.0–1.2)	4		Ps	Sc	
Sideritis lagascana	31.2	(29–33)	24.0	(22–26)	1.31	(1.1–1.4)	4	Simple	Ps	Sc	188
Sideritis lanata	29.7	(29–33)	28	(26–31)	1.07	(0.9–1.6)	4		Ps	Sc	
Sideritis libanotica	28.6	(26–31)	28.6	(26–31)	1.00	(—)	6		Ps	Sc	
Sideritis marshchalliana	30.5	(29–33)	30.5	(29–33)	1.00	(—)	6		Ps	Sc	
Sideritis montana	26.4	(24–29)	25.7	(20–29)	1.03	(0.9–1.3)	3		Ps	Sc+Fo	195, 196
Sideritis pullulans	35.2	(31–40)	35.2	(33–37)	1.00	(0.9–1.1)	6		Ps	Sc	
Sideritis romana	26.0	(24–29)	21.3	(20–24)	1.22	(1.1–1.3)	4		Ps	Sc	189
Sideritis villosa	30.7	(29–33)	28.4	(26–31)	1.07	(0.9–1.2)	4		Ps	Sc	190
Stachyopsis oblongata	23.3	(22–24)	21.6	(20–24)	1.09	(0.9–1.2)	3	Simple	Su	Sc	197–199
Stachys riddellii							3		Su	Sc	200, 201
Stachys sylvatica	28.2	(26–31)	24.4	(24–26)	1.15	(1.1–1.3)	3	Simple	Su	Sc	202–204
Stenogyne haliakalae	39.6	(35–44)	36.5	(33–42)	1.09	(1.0–1.2)	3	Branched?	Su	Sc	205, 206
Stenogyne kamehamehae	45.8	(44–48)	41.4	(40–44)	1.11	(1.0–1.2)	3		Su	Sc	207, 208
Stenogyne purpurea	38.5	(33–44)	31.7	(28–35)	1.22	(1.0–1.4)	3	Simple	Su	Sc	209, 210
Sulaimania otostegioides	21.6	(20–22)	20.0	(19–22)	1.08	(0.9–1.1)	3		Su	Sc	211

TABLE 2. Continued.

Species	Polar axis (μm)		Equatorial axis (μm)		P/E ratio		Colpi	Columellae	Sculpturing		Figures
	Mean	Range	Mean	Range	Mean	Range			Upper	Lower	
Suzukia luchuensis	27.1	(24–29)	24.2	(22–26)	1.12	(1.0–1.3)	3		Su	Sc	212, 213
Synandra hispidula	40.3	(39–42)	30.8	(29–33)	1.31	(1.2–1.4)	3	Simple	Su	Sc	214, 215
Thuspeinanta persica	39.6	(33–42)	29.7	(24–35)	1.35	(1.0–1.6)	3		Su	Sc	216, 217
Wiedemannia orientalis	25.1	(24–29)	18.0	(15–20)	1.40	(1.2–1.7)	3		Su	Sc	218, 219
Subfamily Pogostemonoideae											
Colebrookea oppositifolia	18.7	(18–22)	18.9	(15–20)	0.99	(0.9–1.3)	3	Simple	Su	Sc	240, 241
Comanthosphace japonica	23.5	(22–26)	19.4	(18–22)	1.22	(1.0–1.4)	3		Su	Sc	242–244
Comanthosphace stellipila	24.2	(20–26)	20.0	(18–22)	1.23	(0.9–1.5)	3		Su	Sc	
Comanthosphace sublanceolata	22.0	(20–24)	18.5	(15–22)	1.20	(1.0–1.4)	3		Su	Sc	
Leucosceptrum canum	27.1	(24–29)	24.9	(24–26)	1.09	(1.0–1.2)	3	Simple	Su	Sc	245, 246
Pogostemon brachystachyus	26.0	(24–29)	23.1	(22–24)	1.12	(1.1–1.3)	3		Su	Sc	227, 228
Pogostemon cablin	26.0	(—)	24.2	(22–26)	1.09	(1.0–1.2)	3		Su	Sc	229, 230
Pogostemon cruciatus	24.9	(24–26)	26.4	(24–29)	0.95	(0.9–1.0)	3		Su	Mi	231
Pogostemon glaber	24.9	(20–29)	19.4	(18–22)	1.30	(0.9–1.5)	3		Su	Mi	232, 233
Pogostemon heyneanus	27.3	(26–29)	20.2	(18–22)	1.35	(1.2–1.6)	3		Su	Sc	
Pogostemon myosuroides	23.8	(20–24)	17.4	(15–20)	1.37	(1.1–1.6)	3		Su	Mi	234, 235
Pogostemon plectranthoides	27.1	(24–29)	23.5	(20–26)	1.16	(1.1–1.2)	3		Su	Mi	236, 237
Pogostemon sampsonii	24.0	(—)	22.0	(—)	1.10	(—)	3		Su	?	
Pogostemon stellatus	18.7	(15–22)	16.5	(15–18)	1.15	(0.9–1.4)	3		Su	?	
Pogostemon yatabeanus	24.2	(22–26)	18.7	(15–22)	1.31	(1.0–1.7)	3		Su	Mi	238, 239
Rostrinucula dependens	23.1	(22–26)	21.8	(20–22)	1.06	(1.0–1.2)	3		Su	Sc	247
Genera of uncertain affinities											
Anisomeles heyneana	27.0	(24–29)	25.1	(22–29)	1.09	(0.9–1.3)	3		Su	Mi	220
Anisomeles indica	31.2	(29–35)	32.1	(29–35)	0.98	(0.8–1.2)	3		Su	Mi	221, 222
Anisomeles malabarica	35.2	(33–40)	34.1	(31–37)	1.04	(0.9–1.3)	3		Su	Mi	223
Anisomeles salviifolia	28.2	(26–31)	25.5	(24–26)	1.11	(1.0–1.3)	3		Su	Mi	224, 225
Eurysolen gracilis	23.8	(22–26)	18.9	(18–20)	1.26	(1.1–1.5)	3	Simple	Su	Sc	226

rest of the grain scrobiculate); columellae simple (Nabli, 1976).

POGOSTEMONOIDEAE

Pollen of subfamily Pogostemonoideae (Figs. 227–247) is oblate spheroidal to euprolate, with the polar axis 15–29 μm and the equatorial axis 15–29 μm. The grains are tricolpate and inoperculate. The exine is scrobiculate or microreticulate, with suprareticulate sculpturing (poorly developed in *Rostrinucula*, approaching a psilate condition). In some species of *Pogostemon* (Figs. 231, 235; Pozhidaev, 1989), the lumina contain one or more large central perforations surrounded by small ones. The columellae are unbranched.

DISCUSSION

Pollen morphology provides no distinction between subfamilies Lamioideae and Pogostemonoideae, the variation within the former encompassing that found in the latter. At a lower taxonomic level, similar pollen features suggest relationships within and between certain genera. In some cases, these similarities are thought to be derived, based on a previous cladistic analysis of a more inclusive study group (Cantino, 1992a; see below), and can therefore be cited as putative synapomorphies (de Pinna, 1991) until they are tested for congruence with other characters through a parsimony analysis. Other features are not clearly ancestral or derived and therefore contribute only to an assessment of phenetic relationship.

Based on outgroup comparison to the Scrophulariales, we argued (Abu-Asab & Cantino, 1992) that the following pollen character states are plesiomorphic in the Labiatae: three apertures, absence of operculum, simple columellae, psilate exine. We further hypothesized that suprareticulate sculpturing is a synapomorphy of a large clade comprising the gynobasic-styled Labiatae (including all taxa under study here), some of the genera of Labiatae that lack a gynobasic style, and a few genera traditionally assigned to the Verbenaceae. This hypothesis was corroborated by a cladistic analysis of 85 characters (Cantino, 1992a), five of which pertained to pollen. Within the clade marked by suprareticulate pollen, subfamilies Lamioideae and Pogostemonoideae occupy a relatively derived position. Therefore, although suprareticulate sculpturing is apomorphic in the Labiatae as a whole, it is plesiomorphic within the groups of concern here (Cantino, 1992a). Thus, the plesiomorphic pollen type in subfamilies Lamioideae and Pogostemonoideae is tricolpate, inoperculate, with suprareticulate sculpturing and simple columellae. All of the Pogostemonoideae, most Lamioideae, and the two genera of uncertain affinities exhibit these plesiomorphic conditions, but the following derived states occur in some Lamioideae: tetracolpate and 6-pantocolpate pollen, branched columellae, and four forms of sculpturing (psilate, granulate, rugulate, and suprareticulate-rugulate).

NUMBER OF APERTURES

Within the study group, hexapantocolpate pollen (Figs. 191, 194) was found in *Sideritis* sect. *Empedoclea*. Elsewhere in the family, this feature has been reported in only three species (traditionally assigned to the Verbenaceae but treated here as Labiatae, following Cantino et al., 1992): *Caryopteris nepalensis* Moldenke, *Clerodendrum citrinum* Ridley, and *Huxleya linifolia* Ewart & B. Rees (Abu-Asab et al., 1993). These species are only distantly related to subfamily Lamioideae (Cantino, 1992a). Because 6-pantocolpate pollen is a derived condition (Cantino, 1992a), it can be treated as a putative synapomorphy of *Sideritis* sect. *Empedoclea* pending a test for congruence with other characters. Although we examined only five species, Huynh (1972) studied many others and found this feature to be constant within the section and absent elsewhere in the genus.

Tetracolpate grains (a derived state) were observed in *Haplostachys*, *Marrubium anisodon*, and many species of *Sideritis*. In *Haplostachys*, the colpi are arranged in two pairs (Fig. 53), whereas the colpi are equally spaced in *Sideritis* (Figs. 182, 186, 189); the colpal arrangement in *Marrubium anisodon* is unclear (Fig. 122). In *Sideritis*, tetracolpate pollen delimits a clade comprising four of the six sections (Huynh, 1972). In both examined species of *Haplostachys*, tricolpate and tetracolpate grains were found in the same flower, thus their presence may not be a reliable feature of the genus.

COLUMELLAR STRUCTURE

Simple columellae are plesiomorphic and found in most gynobasic-styled Labiatae (Abu-Asab & Cantino, 1992). The only apparent exceptions we are aware of within the Lamioideae or Pogostemonoideae are *Gomphostemma* (Figs. 66, 72), *Bostrychanthera* (Pozhidaev, 1989), *Chelonopsis lichiangensis* (Fig. 32), and perhaps *Stenogyne haliakalae* Wawra (Fig. 206). In the latter, some columellae seem to branch apically while others appear to be simple. It is unclear from the few available photographs whether the branched struc-

tures are columellae or elements of the tectum. Further TEM study of these genera would help clarify the situation.

It is noteworthy that three of the genera in which these branched structures have been observed (viz., *Bostrychanthera*, *Gomphostemma*, and *Stenogyne*) are members of tribe Prasieae sensu Wunderlich (1967) (= subfamily Prasioideae sensu Briquet, 1895–1897), a group of six genera distinguished by fleshy nutlets. The columellar structure should be examined in the other three genera (*Haplostachys*, *Phyllostegia*, and *Prasium*), and further study of *Chelonopsis* would be worthwhile. Branched columellae (if that is indeed what they are) are derived within the Lamioideae and may therefore provide evidence for a relationship between *Chelonopsis* and tribe Prasieae.

DERIVED FORMS OF SCULPTURING

Most of the species studied have supratectal sculpturing of some sort (usually suprareticulate), but the following taxa have psilate pollen: *Lamiophlomis* (Figs. 78, 79), *Marrubium* (Figs. 122–128), *Notochaete* (Figs. 140, 141), *Phlomidoschema* (Figs. 157, 158), *Phyllostegia grandiflora* (Figs. 167, 168), *Sideritis* (Figs. 182–196), and some species of *Gomphostemma* (Figs. 65, 72). Although the term "psilate" is sometimes restricted to tectate pollen, we apply it here to any grain lacking supratectal or supramural sculpturing. Most of the psilate species have a scrobiculate exine (bordering on punctate in some species of *Marrubium* and *Sideritis*), but it is reticulate in *Phyllostegia grandiflora* and microreticulate in *Gomphostemma intermedium*. In *Sideritis montana* (Figs. 195, 196) and *S. remota* (Huynh, 1972), foveolate zones are localized in five distinct areas, two at the poles and three on the mesocolpia; the rest of the surface is scrobiculate.

The evolution of psilate grains in the Lamioideae is a reversal because suprareticulate sculpturing (plesiomorphic in the Lamioideae) evolved from psilate ancestors (Abu-Asab & Cantino, 1992; Cantino, 1992a). One must be cautious about inferring relationships based on this feature because the transformation of suprareticulate to psilate grains has occurred several times in the Labiatae (Wagstaff, 1992). An intermediate condition may be represented in one genus of Lamioideae (*Metastachydium*, Fig. 121) and one of Pogostemonoideae (*Rostrinucula*, Fig. 247). Two of the genera with psilate pollen (*Sideritis* and *Marrubium*) have long been grouped together on the basis of floral morphology (Bentham, 1832–1836, 1876; Briquet, 1895–1897), but the other psilate taxa are not thought to be related to them.

The psilate pollen of *Lamiophlomis* supports (at least on phenetic grounds) its segregation from *Phlomis*, as pointed out by Azizian & Moore (1982), and the psilate pollen of *Phlomidoschema* supports its segregation from *Stachys*. In all such cases in which a genus is segregated on the basis of a putative apomorphy, its segregation is provisional pending phylogenetic study of the larger complex it belongs to. Ideally, it should be demonstrated that both the segregate and the taxon it is segregated from have synapomorphies; otherwise removal of the segregate may create a paraphyletic group.

The distribution of granulate sculpturing may be systematically significant in *Gomphostemma*, *Lamium*, and *Phlomis*. Within the latter, it was found only in *P. maximoviczii* and *P. umbrosa* (Figs. 163, 166). The other species of *Phlomis* that we examined, the five species studied by Ubera & Galán (1983), and the six species of *Phlomis* s. str. (i.e., excluding *P. rotata* Benth. [= *Lamiophlomis*]) illustrated by Azizian & Moore (1982) all have suprareticulate pollen. The species with granulate pollen (also the smallest grains in the genus; Table 2) are both found in northern China and belong to section *Phlomoides* (Moench) Briq. (Briquet, 1895–1897). Other species in this section have suprareticulate pollen (e.g., *P. agraria*, Figs. 159, 160; Azizian & Moore, 1982).

Within *Lamium*, both species with granulate sculpturing (*L. album* and *L. moschatum*) fall within section *Lamiotypus* Dumort. sensu Mennema (1989). More generally, the variation in sculpturing found in Lamium correlates well with Mennema's classification. This is not the case in *Gomphostemma*, where the distribution of sculpturing types is incongruent with the sectional classification used by Briquet (1895–1897) and Wu & Li (1977). The two species with granulate sculpturing (*G. chinense* and *G. parviflorum*) fall into different sections. At least three sculpturing types (Figs. 63, 65, 70) are represented within section *Gomphostemma* and two (Figs. 68, 74) within section *Stenostoma* Prain.

Rugulate sculpturing was found in *Gomphostemma javanicum* (Fig. 70) and *Lagopsis marrubiastrum* (Fig. 77). Although both are described here as rugulate, the sculpturing is quite different in appearance. Moreover, the rugulate sculpturing in *Lagopsis* is confined to the mesocolpium; the surface becomes psilate toward the poles. It would be worth determining whether this unique pollen type occurs in the other three species of *Lagopsis*,

as it may be a synapomorphy for the genus and supporting evidence for its segregation from *Marrubium*. All examined species of *Marrubium* s. str. have psilate pollen (Figs. 122–128).

Suprareticulate-rugulate sculpturing, found in *Paraphlomis javanica* (Fig. 153), is marginally distinct from suprareticulate; it differs in that the undulating muri are discontinuous in places and do not consistently anastomose to form lumina, so the supratectal ornamentation varies from reticulate to rugulate on a single grain; furthermore, the muri are granulate (more apparent in the micrographs of Azizian & Moore (1982)). *Paraphlomis oblongifolia* (Blume) Prain has similar sculpturing but with more densely granulate muri (Azizian & Moore, 1982); the other two species of *Paraphlomis* studied have suprareticulate sculpturing (Figs. 155, 156).

VARIANTS OF SUPRARETICULATE SCULPTURING

Within the general class of surpareticulate sculpturing, there is variation in the shape and height of the muri, the size and shape of the lumina, and the number, size, shape, and arrangement of the perforations. It is difficult to assess the polarity of these characters due to variation in the outgroups, but similarities in the sculpturing of certain taxa deserve comment.

The similar sculpturing of *Lamium galeobdolon* (Fig. 87) and *L. flexuosum* (Fig. 82) supports Mennema's (1989) circumscription of *Lamium* subg. *Galeobdolon* (Adans.) Asch. *Lamium galeobdolon* is frequently segregated as the genus *Galeobdolon* Adans. or *Lamiastrum* Heist. ex Fabr., but pollen morphology supports its inclusion within *Lamium*.

The Japanese endemic *Ajugoides humilis* has been variably assigned to *Ajuga*, *Lamium*, *Loxocalyx*, *Stachys*, and the monotypic *Ajugoides* (Kudo, 1929). Its suprareticulate exine sculpturing, with large and sometimes incomplete lumina (Fig. 13), does not resemble that of *Ajuga* (Abu-Asab & Cantino, 1993a), *Lamium* (Figs. 80–91), *Loxocalyx* (Figs. 101–103), or most species of *Stachys* (Figs. 200–204; Bassett & Munro, 1986; Demissew & Harley, 1992). Similar sculpturing occurs in one Mexican species of *Stachys* (*S. tenerrima* Epling; figs. 19, 20 of Bassett & Munro, 1986) and some species of *Scutellaria* (Abu-Asab, 1990). *Ajugoides* is unlikely to be closely related to *Scutellaria*, from which it differs greatly in flower and fruit morphology. It is best retained for now as a monotypic genus, but a relationship to *Stachys* should be investigated.

The only endemic North American genera in subfamily Lamioideae are four members of subtribe Melittidinae sensu Bentham (1848): *Brazoria*, *Macbridea*, *Physostegia*, and *Synandra*. Similarity in stomatal configurations (Cantino, 1990) suggests that *Brazoria*, *Physostegia*, and *Macbridea* form a clade. However there is only weak support for a relationship between these three genera and *Synandra* (Abu-Asab & Cantino, 1987), and no evidence that the remaining genera of Melittidinae, *Melittis* (European) and *Chelonopsis* (Eastern Asian), are related to the four North American genera. A similar picture emerges from the pollen data. Neither *Chelonopsis* (Figs. 31–34) nor *Melittis* (Figs. 119, 120) resembles any of the North American Melittidinae in pollen morphology. The exine sculpturing is quite similar in *Brazoria* (Figs. 23–27), *Macbridea* (Figs. 104–106), and *Physostegia* (Figs. 175, 176; for higher magnification, see Cantino, 1982; Trudel & Morton, 1992). All three have unusually minute perforations and angular muri; in *Physostegia* and some species of *Brazoria*, the shallow lumina are bounded by gradually sloping muri.

Synandra (Fig. 214) differs in sculpturing from *Macbridea*, *Brazoria*, and *Physostegia* but resembles *Galeopsis* (Figs. 46–50). Although a close relationship between *Synandra* and *Galeopsis* has not previously been suggested, they share a distinctive form of suprareticulate sculpturing, with elongate perforations that tend to radiate out from the center of well-defined lumina. Moreover, *Synandra* and *Galeopsis* share two putative synapomorphies. Both are monocarpic (*Galeopsis* is annual and *Synandra* biennial), a derived condition in the Labiatae (Cantino, 1992a). Both have distinct anther thecae; confluent thecae are plesiomorphic in the Lamioideae (Cantino, 1992a).

GENERA OF UNCERTAIN AFFINITIES

Two genera of uncertain subfamilial affinities, *Anisomeles* and *Eurysolen*, were included in the study with the hope that pollen morphology might clarify their position. The monotypic genus *Eurysolen* has been assigned to widely divergent positions in the Labiatae. It was described by Prain (1898), who placed it in the Prasieae (Lamioideae) near *Gomphostemma*. Mukerjee (1940) and Wu & Li (1977) placed *Eurysolen* in the Ajugoideae. Keng (1969) noted a close resemblance to *Achyrospermum* (Lamioideae) in general habit, inflorescence, and floral structure. Press (1982) included the genus within the Pogostemonoideae and pointed out similarities with *Pogostemon*, *Rostrinucula*, and *Comanthosphace*. Unfortunately, pol-

len morphology is of little help in resolving the affinities of *Eurysolen*. Its sculpturing (Fig. 226) resembles species of *Achyrospermum* (Fig. 4), *Comanthosphace* (Fig. 244), and *Ajuga* (Abu-Asab & Cantino, 1993a).

Anisomeles was assigned by Bentham (1848, 1876) and Briquet (1895–1897) to tribe Lamieae (corrected nomenclature follows Sanders & Cantino, 1984), but it lacks characteristic embryological and chemical traits of subfamily Lamioideae (Wunderlich, 1967; Abu-Asab & Cantino, 1987; Cantino, 1992a). Cantino (1992a, b) hypothesized a close relationship between *Anisomeles* and *Pogostemon* based on three synapomorphies: presence of subsessile leaf epidermal glands with a unicellular cap, bearded stamen filaments, and a lustrous pericarp. On the basis of this evidence, Cantino et al. (1992) provisionally assigned *Anisomeles* to subfamily Pogostemonoideae. The distinctive suprareticulate sculpturing of *Anisomeles*, with its regular, polygonal lumina and relatively large perforations (Figs. 220–225), is very similar to that of Pogostemon (Figs. 227–239), supporting the hypothesized relationship between these genera. Within the Lamioideae, similar sculpturing was found in some species of *Microtoena* (Figs. 129–136).

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APPENDIX. Abbreviated collection data for voucher specimens. Herbarium abbreviations follow Holmgren et al. (1990).

Achyrosperumum aethiopicum Welw.—Malawi, Pumphi District, *Pawek 6606* (MO).

Achyrospermum carvalhi Gürke—Malawi, *LaCroix 3058* (MO).

Achyrospermum cryptanthum Baker—Tanzania, *Frame 44* (MO).

Achyrospermum densiflorum Blume—Thailand, Southwest Province, Kanchanaburi District, *van Beusekom et al. 3739* (K).

Achyrospermum parviflorum S. Moore—Uganda, *Loveridge 217* (MO).

Achyrospermum schimperi (Hochst. ex Briq.) Perkins—Ethiopia, Shoa Province, *Ash 1726* (MO).

Acrotome angustifolia G. Taylor—Zambia, Barotseland, *Robinson 6789* (MO).

Acrotome hispida Benth.—South Africa, Transvaal, *Werdermann & Oberdieck 1281* (A).

Acrotome inflata Benth.—Botswana, *Galloway 505* (MO).

Acrotome fleckii (Gürke) Launert—Namibia, *Seydel 2675* (A).

Ajugoides humilis (Miq.) Makino—Japan, Yama-jio, *Anonymous* (US 350854); Nagasaki, *Maximowicz s.n.* (BM).

Alajja rhomboidea (Benth.) Ikonn.-Gal.—Afghanistan, Kurrum Valley, *Aitchison 831* (GH).

Anisomeles heyneana Benth.—India, Mumbra, 2 Dec. 1950, *Santapau s.n.* (MO).

Anisomeles indica (L.) Kuntze—India, Hassan District, *Saldanha & Gandhi 2170* (MO). China, Hainan, *Chun & Tso 43882* (MO).

Anisomeles malabarica (L.) R. Br. ex Sims—India, Hassan District, *Saldanha 16079* (MO).

Anisomeles salviifolia R. Br.—Australia, Northern Territory, *Adams 1755* (K).

Ballota africana Benth.—South Africa, *Perry & Snijman 2313* (MO).

Ballota andreuzziana Pamp.—Libya, Kouf National Park, "*J.H.H. L67*" (K).

Ballota hirsuta Benth.—Morocco, N of Tafraoute, "*B. M. Exped. 422*" (MO).

Ballota integrifolia Benth.—Cyprus, Paphos District, *Davis 3405* (K).

Ballota nigra L.—U.S.A., Ohio, Athens County, *Cantino 1300* (BHO). Italy, Cicilia, *Larsen, Larsen & Nielsen 35996* (MO).

Ballota pseudodictamnus (L.) Benth.—U.S.A., Ohio, Athens (cultivated), *Cantino 1329* (BHO).

Ballota rupestris (Biv.) Vis.—U.S.A, Ohio, Athens (cultivated), *Cantino 1310* (BHO).

Brazoria arenaria Lundell—U.S.A, Texas, Aransas County, *Kessler 5773* (BHO).

Brazoria pulcherrima Lundell—U.S.A, Texas, Leon County, *Kessler 5865* (BHO).

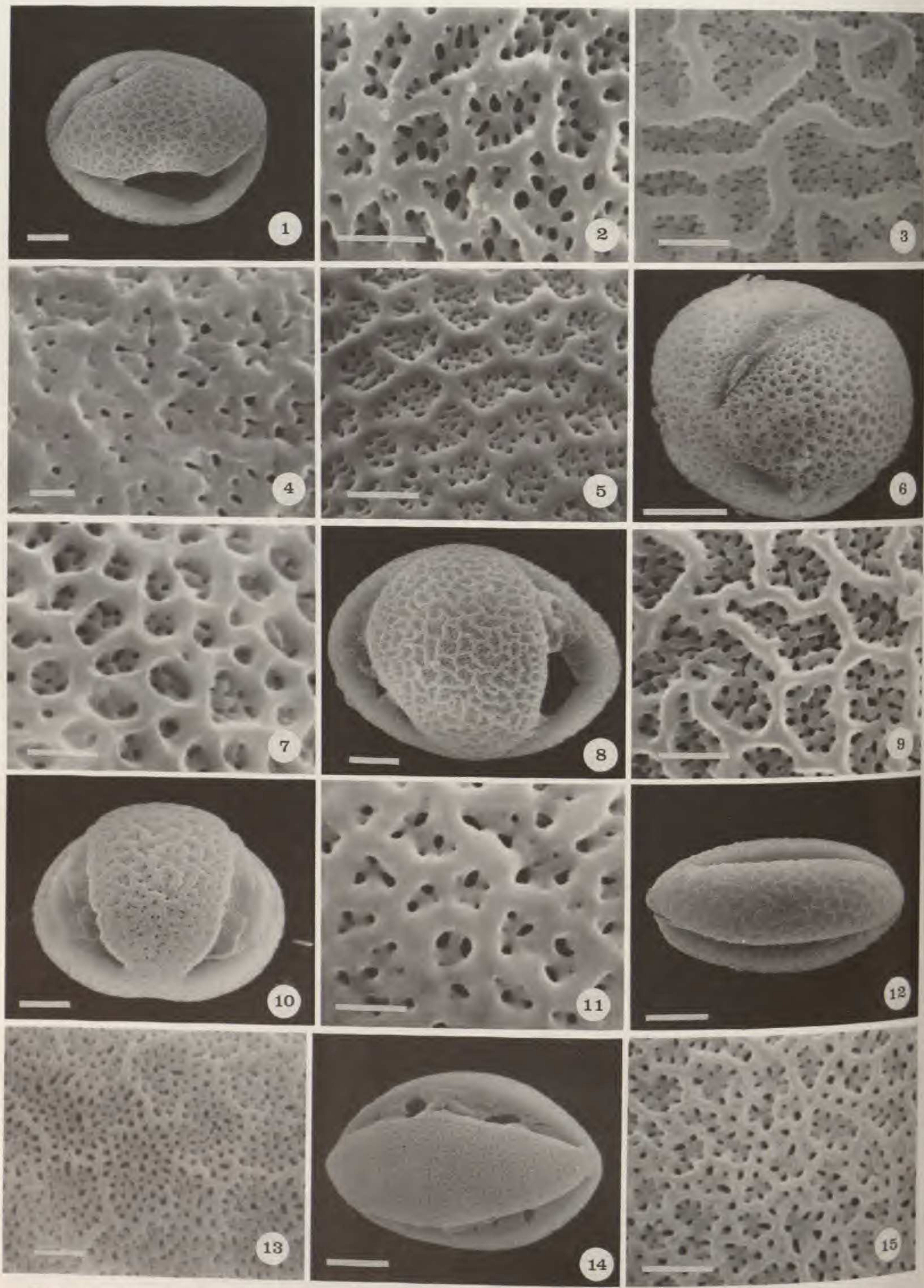
Brazoria scutellarioides Engelm. & A. Gray—U.S.A. Texas, Barton Creek, 15 May 1936, *Tharp s.n.* (GH); Travis County, *Sanders 76179* (TEX).

Brazoria truncata (Benth.) Engelm. & A. Gray—U.S.A.,

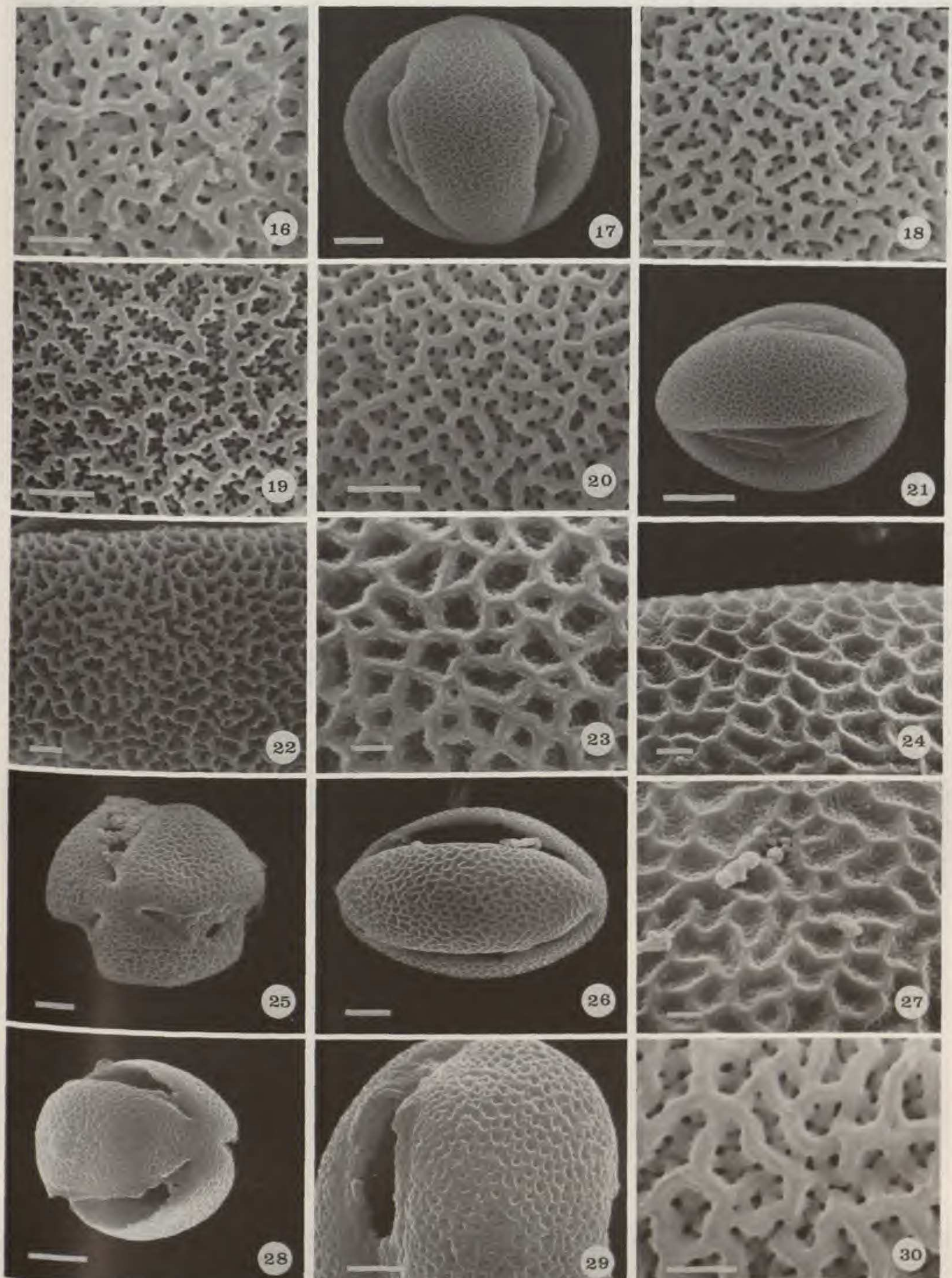
Texas, Live Oak County, *Sanders 76122* (TEX); Burnet County, *Correll & Ogden 25300* (GH).
Chamaesphacos ilicifolius Schrenk—Iran, E Khorasan, *Rechinger 51448* (MO).
Chaiturus marrubiastrum (L.) Spenner—U.S.A., Kansas, Douglas County, *McGregor 12* (US).
Chelonopsis lichiangensis W. Smith—China, Yunnan, *Forrest 15429* (K).
Chelonopsis odontochila Diels—China, Yunnan, Chungtien, *Yu 14923* (A).
Colebrookea oppositifolia Smith—China, Yunnan, *Rock 2348* (A).
Colquhounia coccinea Wallich—China, Yunnan, *Rock 6231* (A).
Colquhounia seguinii Vaniot—China, Yunnan, *Ten 26* (A).
Comanthosphace japonica (Miq.) S. Moore—Japan, Tochigi Pref., 10 Sep. 1975, *Ohashi & Murata s.n.* (A). Japan, 1862, *Anonymous* (US).
Comanthosphace stellipila (Miq.) S. Moore—Japan, Suruga Province, Shidzuoka Pref., 30 Aug. 1958, *Furuse s.n.* (A). Japan, *Makino s.n.* (US).
Comanthosphace sublanceolata (Miq.) S. Moore—Japan, Hondo, *Shiota 7301* (GH).
Craniotome furcata (Link) Kuntze—Nepal, *Banerjo 2864* (US). Nepal, Riala, *Polunin, Sykes & Williams 1297* (A). India, NW Himalayas, *Gupta s.n.* (US).
Eremostachys fetissovii Regel—Kazakhstan, *Goloskokov 4487* (A).
Eremostachys iliensis Regel—Kazakhstan, *Goloskokov 4143* (A).
Eremostachys rotata Schrenk ex Fischer & C. Meyer—Kazakhstan, *Roldugin 4432* (A).
Eremostachys speciosa Rupr.—Kirghizia, *Armand 961* (A).
Eriophyton wallichianum Benth.—China, Tibet, *Ludlow & Sherriff 8859* (GH).
Eurysolen gracilis Prain—Indonesia, Java, *van Steenis 11118* (GH).
Galeopsis bifida Boenn.—Denmark, Zealand, *Svendsen 450* (MO).
Galeopsis ladanum L.—Switzerland, 23 July 1953, *Lohammar s.n.* (MO).
Galeopsis pubescens Besser—Switzerland, Evolene, *Anonymous 3139* (MO).
Galeopsis segetum Necker—U.S.A., Ohio, Athens (cultivated), *Cantino 1339* (BHO).
Galeopsis speciosa Miller—Finland, Nylandia, *Vanhecke 5480* (MO).
Galeopsis tetrahit L.—Canada, Ontario, Algoma District, *Sample & Brammall 2864* (MO).
Gomphostemma chinense Oliver—Thailand, Banang Sta., *Kerr 7346* (K).
Gomphostemma intermedium Craib—Thailand, *Kerr 6347* (K).
Gomphostemma javanicum (Benth.) Benth.—Malaysia, Pahang, *Shah 2772* (A).
Gomphostemma leptodon Dunn—Indochina, Dec. 1926, *Anonymous 5002* (A).
Gomphostemma lucidum Wallich ex Benth.—Thailand, Dai Angka, *Garrett 409* (K).
Gomphostemma parviflorum Wallich ex Benth.—Bangladesh, Chittagong, *Parkinson 4263* (A).
Gomphostemma wallichii Prain—Burma, *J. F. Smith 107* (GH).
Haplostachys haplostachya (A. Gray) H. St. John—U.S.A., Hawaii, Waimea, *Rock 8350* (A).
Haplostachys linearifolia (Drake) Sherff—U.S.A., Hawaii, Mauna Loa, Molokai, Feb. 1910, *Rock s.n.* (GH).
Hypogomphia turkestana Bunge—Afghanistan, Salang Pass, *Hewer 1025A* (K). USSR, Turgaiskaia, *Krascheninnikov 5127* (A).
Lagochilus aucheri Boiss.—Iran, Kurdistan, *Rechinger 42853* (K).
Lagochilus diacanthophyllus (Pallas) Benth.—Kazakhstan, *Goloskokov 5788* (MO).
Lagochilus hirtus Fischer & C. Meyer—Kazakhstan, *Goloskokov 4292* (MO).
Lagopsis marrubiastrum (Stephan) Ikonn.-Gal.—India, *Koelz 6565* (US).
Lagopsis supina (Stephan) Ikonn.-Gal.—China, Hebei, *Beach 17* (K).
Lamiophlomis rotata (Benth.) Kudo—China, Tibet, *Rock 14406* (GH).
Lamium album L.—Iceland, Knappstadhir, *Elseley 55/71* (MO).
Lamium flexuosum Ten.—Italy, Sicilia, *Larsen 35657* (MO).
Lamium galeobdolon (L.) L.—Britain, S Wales, 11 May 1964, *Price s.n.* (MO).
Lamium garganicum L.—Turkey, Malatya, *Balls B2287* (K).
Lamium moluccellifolium Fries—Denmark, Ega District, 26 June 1966, *Benjamin s.n.* (MO).
Lamium moschatum Miller—Cyprus, Liveras, *Meikle 2410* (K).
Lamium purpureum L.—U.S.A, Ohio, Athens County, *Cantino 1273* (BHO).
Leonotis bequaertii De Wild.—Zaire, Katanga Province, Momba Territory, *Dubois 1072* (K).
Leonotis leonitis R. Br.—Kenya, Machakos District, *Verdcourt 2362* (K).
Leonotis mollissima Gürke—Tanzania, Monduli District, *Greenway & Kanuri 12560* (K).
Leonurus cardiaca L.—U.S.A, Minnesota, Houston County, *Swanson 811* (MO). Mexico, Chiapas, *Lellez & Pankhurst 6966* (MO).
Leonurus sibiricus L.—Honduras, *Nichols 2140* (MO).
Leucas abyssinica (Benth.) Briq.—Somalia, Luuq District, *Wieland 1142* (MO).
Leucas alluaudii Sacleux—Burundi, Muramwya, Teza, *Reekmans 10728* (MO).
Leucas aspera (Willd.) Link—China, Hainan, Janfengling, *Chow 78309* (MO).
Leucas biflora R. Br.—Sri Lanka, Yala Bungalow, *Cooray 69010407R* (MO).
Leucas calostachys Oliver—Burundi, Muyinga Province, *Reekmans 6977* (MO).
Leucas ciliata Benth.—India, Hassan District, *Ramamoorthy & Gandhi HFP2602* (MO).
Leucas eriostoma Hook. f.—India, Karnataka Chikmagalur, *Saldanha KFP9600* (MO).
Leucas hirta Sprengel—India, Hassan District, *Saldanha 17909* (MO).
Leucas inflata Benth.—Yemen, Bait al Lakida, *Miller 12* (K).
Leucas javanica Benth.—Indonesia, Celebes, *Meijer 10953* (MO).
Leucas lanata Benth.—India, Mussoorie, *Dudgeon & Kenoyer 37* (MO).
Leucas lavandulifolia Smith—India, Hassan District, *Ramamoorthy HFP1744* (MO).
Leucas marrubioides Desf.—India, *Bembower 169* (MO).

Leucas martinicensis R. Br.—India, Hassan District, Mysore, *Saldanha 15337* (MO).
Leucas mollissima Wallich ex Benth.—Japan, Kagoshima Prefecture, Pyukyu, *Iwatsuki et al. 104* (MO).
Leucas rosmarinifolia Benth.—India, Kodaikanal, *Bembower 331* (MO).
Leucas stelligera Wallich—India, Castle Rock, *Almeida 257* (MO).
Leucosceptrum canum Smith—China, Yunnan, *Rock 6650* (A). Burma, *McMillen 196* (US).
Loxocalyx ambiguus (Makino) Makino—Japan, Yamato Province, *Murata 10748* (A).
Loxocalyx urticifolius Hemsley—China, Hubei, *Henry 6482* (GH).
Macbridea alba Chapman—U.S.A, Florida, Bay County, *Godfrey 79884* (BHO); Apalachicola, *Biltmore Herb. 4199a* (GH).
Macbridea caroliniana (Walter) Blake—U.S.A, North Carolina, Brunswick County, *Radford 6334* (GH).
Marrubium anisodon C. Koch—Afghanistan, Ghorband, *Seybold 36896* (MO).
Marrubium cuneatum Russell—Iraq, Kursi, *Gillett 10852* (K).
Marrubium heterodon (Benth.) Boiss. & Balansa—Turkey, Adana Province, *Davis 16545* (K).
Marrubium incanum Desr.—U.S.A., Ohio, Athens (cultivated), *Cantino 1334* (BHO).
Marrubium supinum L.—Spain, Sierra de Cazorla, *Townsend T46* (K).
Melittis melissophyllum L.—Greece, *Mennega 174* (MO).
Metastachydium sagittatum (Regel) C.Y. Wu & Li—Kirghizia, Tien Shan Mountains, *Medvedeva et al. 251* (A).
Microtoena delavayi Prain—China, Yunnan, *Forrest 15177* (K).
Microtoena insuavis (Hance) Prain ex Briq.—China, Yunnan, *Wang 80582* (A).
Microtoena robusta Hemsley—China, Hubei, *Henry 6482A* (GH).
Microtoena urticifolia Hemsley—China, Yunnan, *McLaren's Collectors P112* (A).
Moluccella laevis L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1328* (BHO).
Moluccella spinosa L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1316* (BHO).
Notochaete hamosa Benth.—India, Assam, *Bor 16154* (A).
Otostegia fruticosa Briq.—Saudi Arabia, *Humbles 10008* (MO).
Otostegia integrifolia Benth.—Ethiopia, *Amshoff 10381* (MO).
Otostegia minuccii Pic.-Serm.—Ethiopia, Addis Ababa, *Meyer 7472* (MO).
Otostegia repanda Benth.—Ethiopia, Sidamo Province, *Ash 1885* (MO).
Otostegia tomentosa A. Rich.—Ethiopia, Debra Zebit, *Boulos 9790* (MO).
Panzerina lanata (L.) Soják—Mongolia, Altai, *Steinberg & Prochorova 3459* (A). Russia, Krasnojarsk Province, *Reverdatto 3775b* (A) [labeled as *Panzeria argyracea*].
Paralamium gracile Dunn—China, Yunnan, *Henry 10636* (K).
Paraphlomis javanica (Blume) Prain ex Backer & Bakh. f.—Indonesia, Sumatra, *Rahmat Si Boeea 9772a* (GH).
Paraphlomis lanceolata Hand.-Mazz.—China, Hunan, Changning Hsien, *Fan & Li 91* (GH).
Paraphlomis rugosa Prain—China, Gwangdong, *Merrill 10741* (A).
Phlomidoschema parviflorum (Benth.) Vved.—Pakistan, Baluchistan, Kurram District, *Siddiqi & Iqbal 94* (A).
Phlomis agraria Bunge—Kazakhstan, *Schipczinsky 802* (A).
Phlomis crinita Cav.—Algeria, Oran Department, *Samuelsson 7071* (GH).
Phlomis herba-venti L.—France, Aude Department, 12 July 1891, *Neyraut s.n.* (GH).
Phlomis lanata Willd.—U.S.A., Ohio, Athens (cultivated), *Cantino 1365* (BHO).
Phlomis maximoviczii Regel—China, Manchuria, *Litvinov 1559* (A).
Phlomis tuberosa L.—U.S.A, Ohio, Athens (cultivated), *Cantino 1294* (BHO).
Phlomis umbrosa Turcz.—China, Shandong Province, *Chiao 2735* (GH).
Phyllostegia grandiflora (Gaudich.) Benth.—U.S.A, Hawaii, Oahu, Palolo Valley, 30 Nov. 1912, *Rock & Ballori s.n.* (GH).
Phyllostegia hirsuta Benth.—U.S.A, Hawaii, Oahu, Mt. Olympus, Apr. 1918, *Rock & Lyon s.n.* (A).
Phyllostegia hispida Hillebr.—U.S.A, Hawaii, Molokai, *Rock 10327* (A).
Phyllostegia lantanoides Sherff—U.S.A, Hawaii, Oahu, *Degener 10038* (GH).
Phyllostegia racemosa Benth.—U.S.A, Hawaii, Molokai, *Rock 6198* (A).
Physostegia longisepala Cantino—U.S.A., Louisiana, Calcasieu Parish, *Gilmore & Smith 3501* (BHO).
Physostegia pulchella Lundell—U.S.A., Texas, Brazoria County, *Brown 9892* (BHO).
Pogostemon brachystachyus Benth.—India, Assam, Khasi Hills, *Hooker & Thomson s.n.* (GH).
Pogostemon cablin (Blanco) Benth.—Puerto Rico, Mayaguez, *Horn 5424* (GH).
Pogostemon cruciatus (Benth.) Kuntze—Nepal, *Strachey & Winterbottom s.n.* (GH).
Pogostemon glaber Benth.—China, Hainan, *McClure s.n.* (Canton Christian College Herb. 8454) (A).
Pogostemon heyneanus Benth.—U.S.A, Ohio, Athens (cultivated), *Cantino 1314* (BHO).
Pogostemon myosuroides (Benth.) Kuntze—India, Malabar Concan, *Stocks, Law & Co. s.n.* (GH).
Pogostemon plectranthoides Desf.—U.S.A, Ohio, Athens (cultivated), *Cantino 1317* (BHO).
Pogostemon sampsonii (Hance) Press—China, Guangdong, Wung Yuen District, *Lau 2549* (GH).
Pogostemon stellatus (Lour.) Kuntze—China, Kwangsi, Kweilin, *Wan & Chow 79176* (A).
Pogostemon yatabeanus (Makino) Press—Japan, Mino Province, Hondo, *Shiota 4267* (GH).
Prasium majus L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1356* (BHO).
Pseuderemostachys sewertzowii (Herder) Popov—Kazakhstan, 12 May 1962, *Karmyscheva s.n.* (MO 1879982).
Rostrinucula dependens (Rehder) Kudo—China, W China, *Wilson 4313* (A).
Roylea cinerea (D. Don) Baillon—India, Chamba District, 27 Apr. 1920, *Parker s.n.* (A).
Sideritis canariensis L.—Spain, Canary Islands, Palma, *Bourgeau 125* (A).
Sideritis candicans Aiton—Spain, Canary Islands, Teneriffe, *Burchard 134* (A).

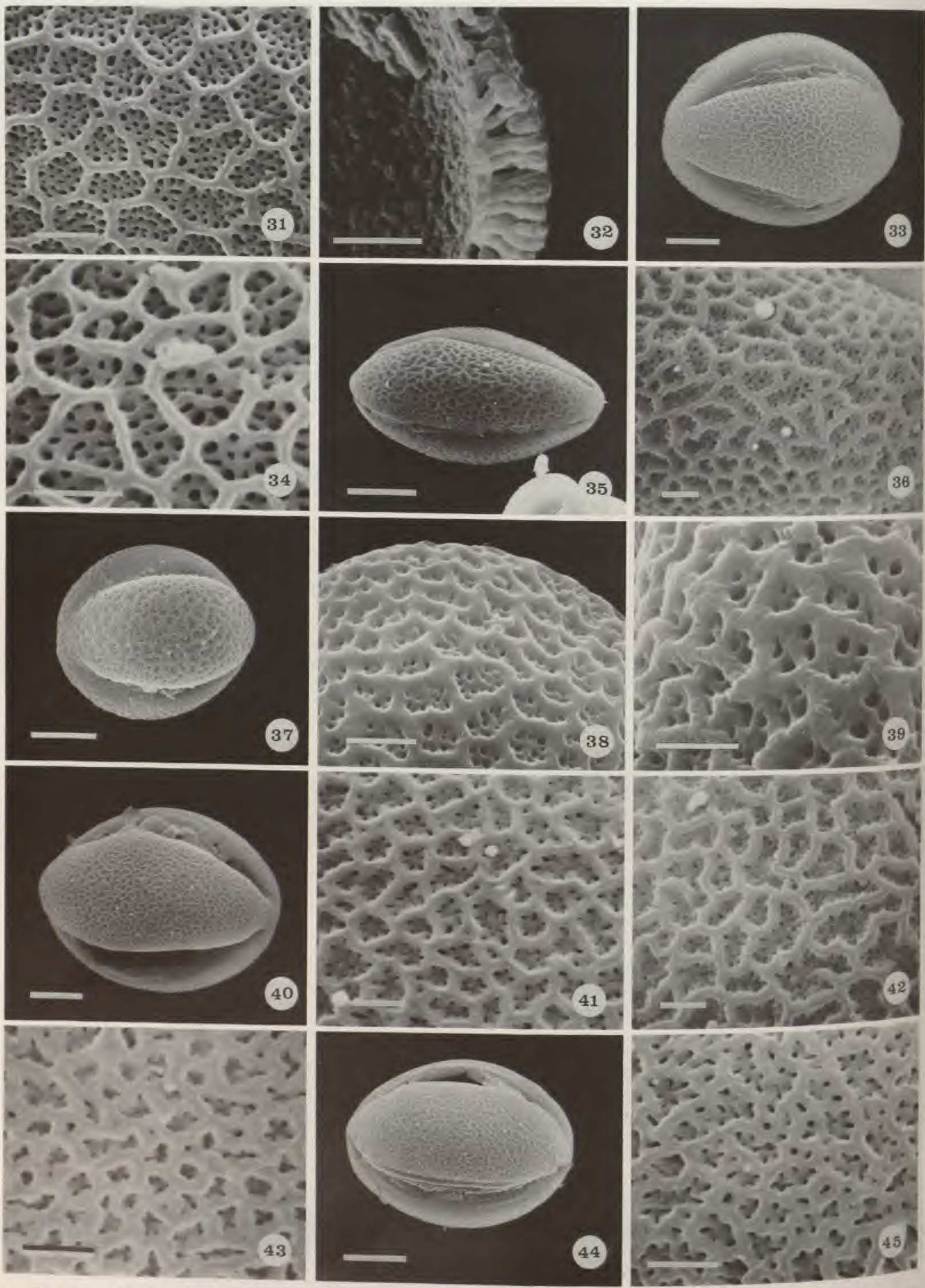
Sideritis chlorostegia Juz.—Ukraine, Crimea, *Juzepczuk 3937* (A).
Sideritis curvidens Stapf—Greece, *Samuelsson & Zander 299* (GH).
Sideritis euboea Heldr.—locality unknown, July 1927, *Purpus s.n.* (A).
Sideritis gomerae Noë ex Bolle—Spain, Canary Islands, 25 May 1894, *Murray s.n.* (K)
Sideritis hirsuta L.—Spain, Aragon, Prov. de Huesca, 20 July 1892, *St. Lager s.n.* (GH).
Sideritis hololeuca Boiss. & Heldr.—Turkey, Konya Province, *Davis 16238* (K).
Sideritis hyssopifolia L.—Spain, Huesca Province, *Brenan 12236* (K).
Sideritis ilicifolia Willd.—Spain, Aragon, Barbastro, 13 July 1892, *St. Lager s.n.* (GH).
Sideritis incana L.—Algeria, 16 July 1894, *Cosson s.n.* (GH).
Sideritis lagascana Willk.—Spain, Granada Province, *Reverchon 1099* (A).
Sideritis lanata L.—Turkey, Bithynia, Bile ik, *Bornmüller 14569* (GH).
Sideritis libanotica Labill.—Syria, *Shepard s.n.* (GH).
Sideritis marschalliana Juz.—Ukraine, Crimea, *Juzepczuk & Vysokoostrovskaja 3939* (A).
Sideritis montana L.—Algeria, Bedeau, 18 June 1934, *Faure s.n.* (GH).
Sideritis pullulans Vent.—Lebanon, *Samuelsson 6150* (MO).
Sideritis romana L.—France, 22 Apr. 1905, *Raine s.n.* (GH).
Sideritis villosa Cosson—Morocco, *Balls B2463* (K).
Stachyopsis oblongata (Schrenk) Popov & Vved.—Afghanistan, Badakshan, *Hedge & Carter 445* (K).
Stachys riddellii House—U.S.A., Ohio, Vinton County, *Cantino 1229* (BHO); Meigs County, Forked Run State Park, *Wistendahl 64-91* (BHO).
Stachys sylvatica L.—U.S.A., Ohio, Athens (cultivated), *Cantino 1364* (BHO).
Stenogyne haliakalae Wawra—U.S.A., Hawaii, Maui, Haleakala National Park, *Olson 5* (K).
Stenogyne kamehamehae Wawra—U.S.A., Hawaii, Molokai, *Degener 5414* (K).
Stenogyne purpurea H. Mann—U.S.A., Hawaii, Kauai, *Degener et al. 23907* (K).
Sulaimania otostegioides (Prain) Hedge & Rech. f.—Pakistan, N Wazir, *Duthie 15788* (K).
Suzukia luchuensis Kudo—Japan, Ryukyu Province, Yaeyama Islands, *Furuse 3205* (K).
Synandra hispidula (Michaux) Baillon—U.S.A, Ohio, Morgan County, *Cantino 1151* (BHO); Lawrence County, *Hammer 6* (BHO).
Thuspeinanta persica (Boiss.) Briq.—Afghanistan, *Aitchison 207* (GH).
Wiedemannia orientalis Fischer & C. Meyer—Turkey, Elazig Province, *Davis & Hedge 28929* (A); Ankara, *Kuntay 48* (MO).



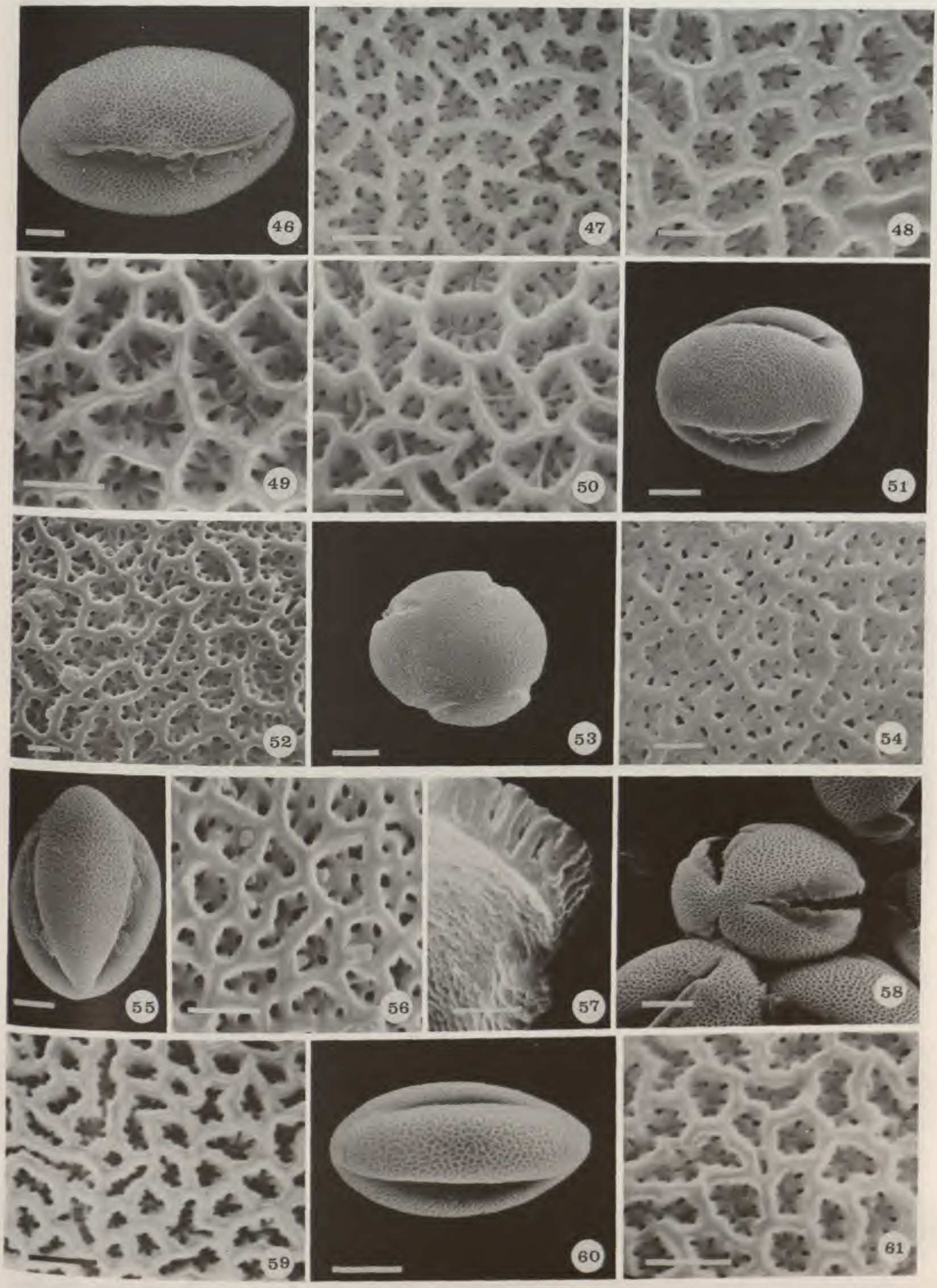
FIGURES 1–15. Pollen of Lamioideae: *Achyrospermum*, *Acrotome*, *Ajugoides*, and *Alajja*.—1, 2. *Achyrospermum aethiopicum*.—3. *Achyrospermum carvalhi*.—4. *Achyrospermum cryptanthum*.—5. *Achyrospermum densiflorum*.—6, 7. *Achyrospermum parviflorum*.—8, 9. *Achyrospermum schimperi*.—10, 11. *Acrotome angustifolia*.—12, 13. *Ajugoides humilis* (*US 350854*).—14, 15. *Alajja rhomboidea*. Scales = 0.5 μm (4); 1 μm (2, 3, 5, 7, 9, 11, 13, 15); 2.5 μm (1, 8, 10); 5 μm (6, 12, 14).



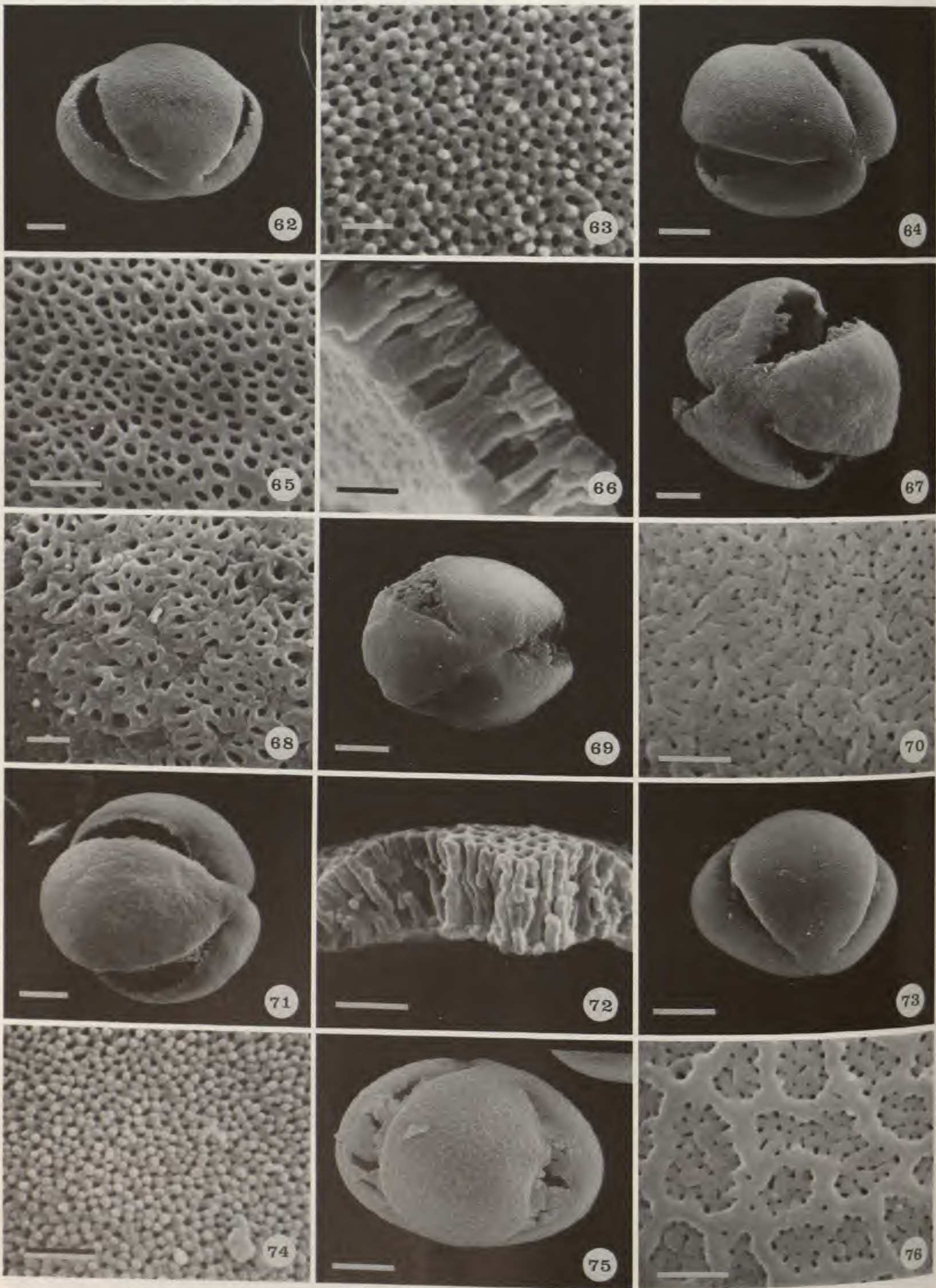
FIGURES 16–30. Pollen of Lamioideae: *Ballota*, *Brazoria*, *Chaiturus*, and *Chamaesphacos*.—16. *Ballota africana*.—17, 18. *Ballota hirsuta*.—19. *Ballota integrifolia*.—20. *Ballota nigra* (*Larsen et al. 35996*).—21, 22. *Ballota pseudodictamnus*.—23. *Brazoria arenaria*.—24. *Brazoria pulcherrima*.—25. *Brazoria scutellarioides* (*Tharp s.n.*).—26, 27. *Brazoria truncata* (*Correll & Ogden 25300*).—28, 29. *Chaiturus marrubiastrum*.—30. *Chamaesphacos ilicifolius*. Scales = 1 μm (16, 18, 19, 20, 22, 23, 24, 27, 30); 2.5 μm (17, 29); 5 μm (21, 25, 26); 10 μm (28).



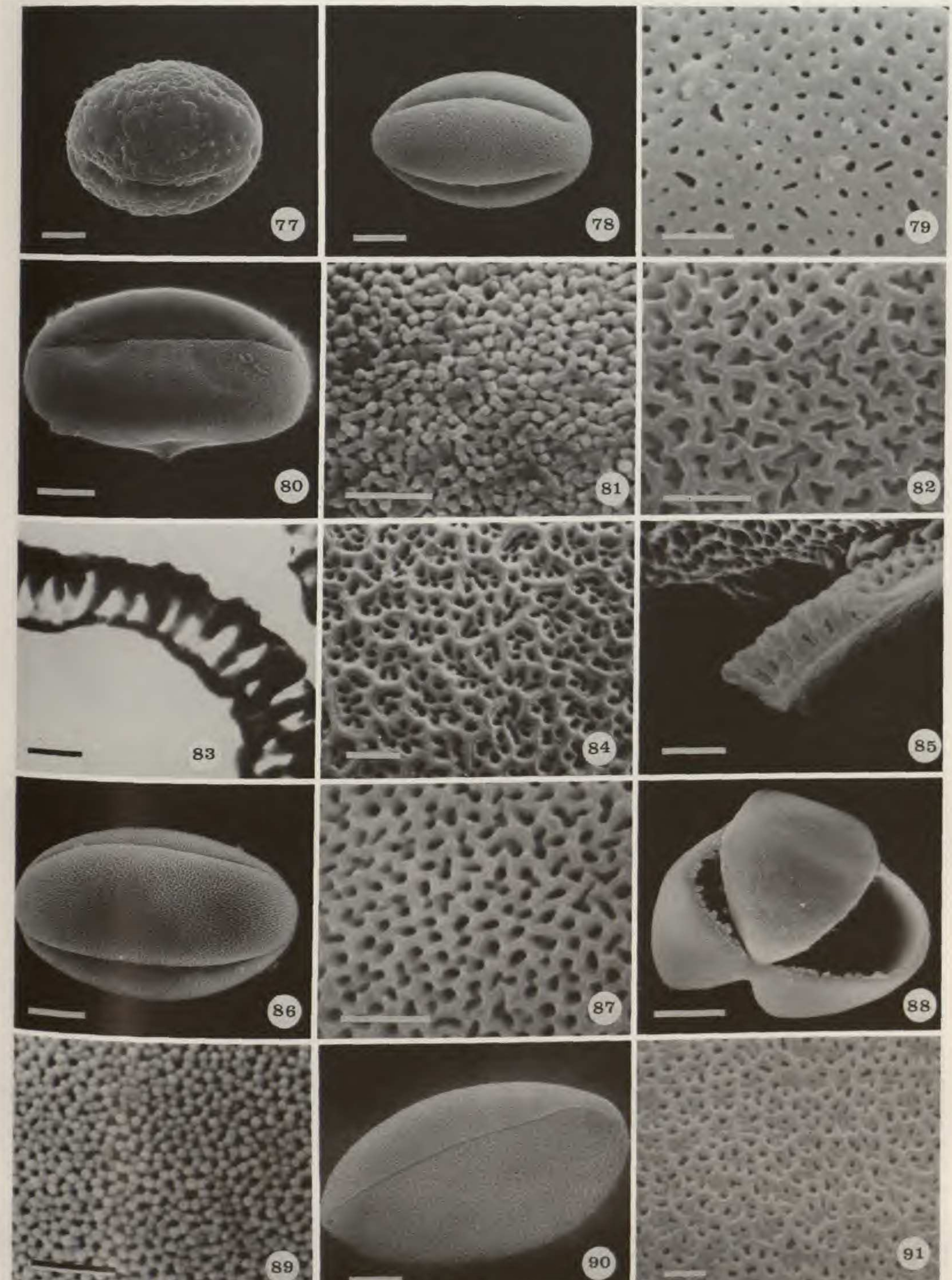
FIGURES 31–45. Pollen of Lamioideae: *Chelonopsis, Colquhounia, Craniotome, Eremostachys,* and *Eriophyton.*—31, 32. *Chelonopsis lichiangensis.*—33, 34. *Chelonopsis odontochila.*—35, 36. *Colquhounia seguinii.*—37, 38. *Craniotome furcata* (*Polunin et al. 1297*).—39. *Craniotome furcata* (*Banerjo 2864*).—40, 41. *Eremostachys iliensis.*—42. *Eremostachys rotata.*—43. *Eremostachys speciosa.*—44, 45. *Eriophyton wallichianum.* Scales = 1 μm (31, 32, 34, 36, 38, 39, 41, 42, 43, 45); 5 μm (33, 35, 37, 40, 44).



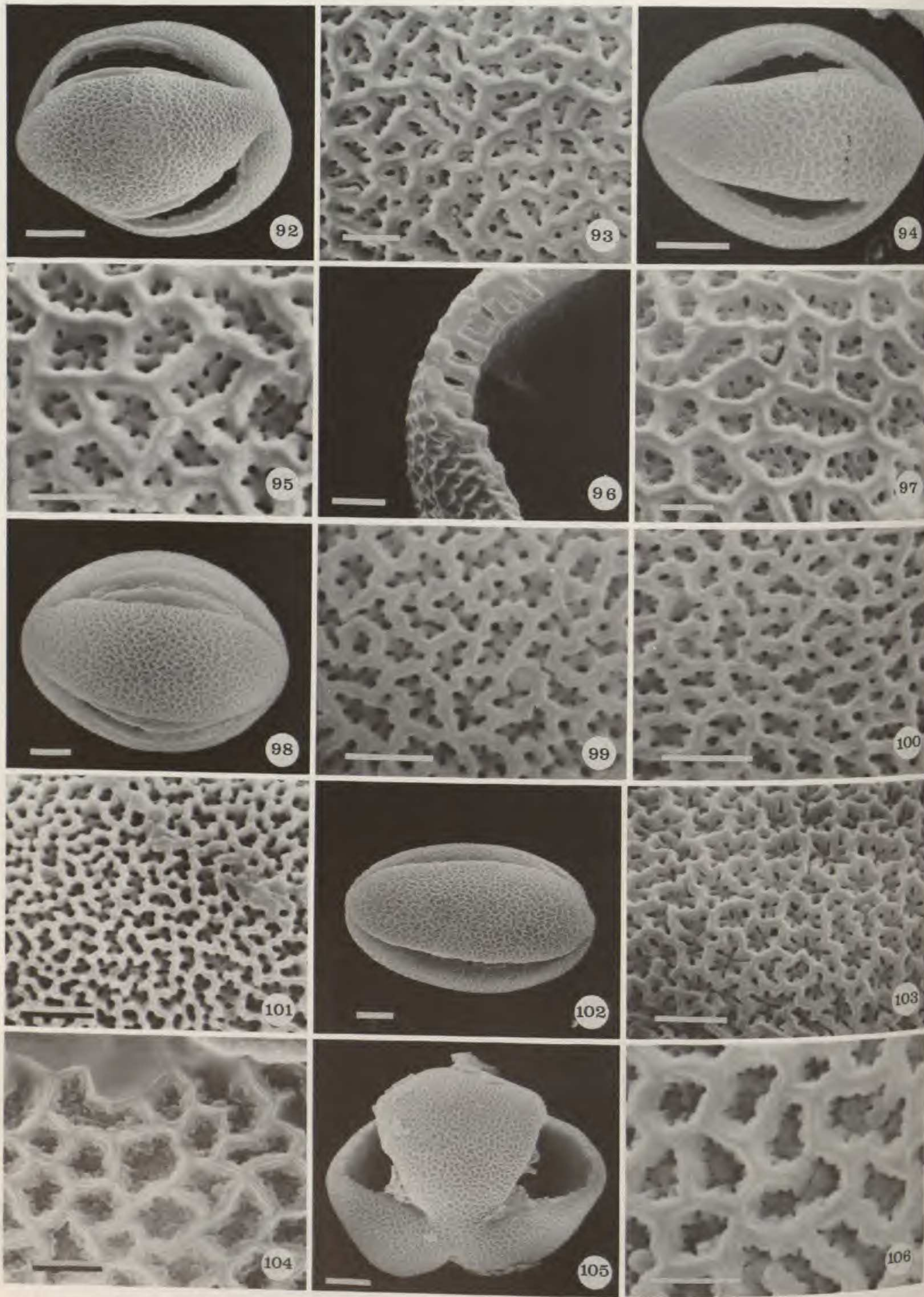
FIGURES 46–61. Pollen of Lamioideae: *Galeopsis, Haplostachys, Hypogomphia,* and *Lagochilus.*—46, 47. *Galeopsis bifida.*—48. *Galeopsis pubescens.*—49. *Galeopsis speciosa.*—50. *Galeopsis tetrahit.*—51, 52. *Haplostachys haplostachya.*—53, 54. *Haplostachys linearifolia.*—55–57. *Hypogomphia turkestana* (*Hewer 1025A*).—58, 59. *Lagochilus aucheri.*—60, 61. *Lagochilus diacanthophyllus.* Scales = 1 μm (47, 48, 49, 50, 52, 54, 56, 57, 59, 61); 5 μm (46, 55, 58, 60); 10 μm (51, 53).



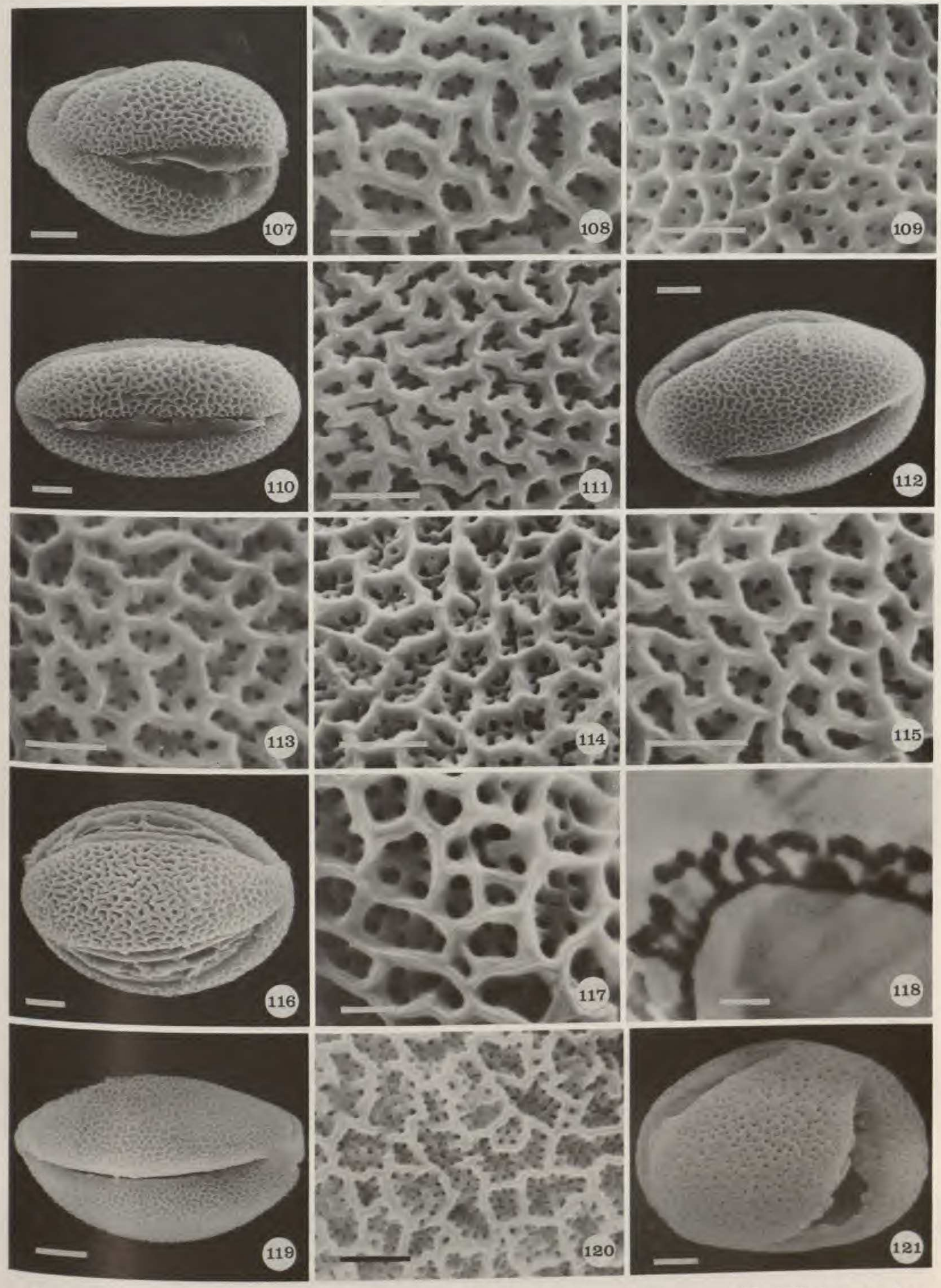
FIGURES 62–76. Pollen of Lamioideae: *Gomphostemma*.—62, 63. *Gomphostemma chinense*.—64–66. *Gomphostemma intermedium*.—67, 68. *Gomphostemma leptodon*.—69, 70. *Gomphostemma javanicum*.—71, 72. *Gomphostemma lucidum*.—73, 74. *Gomphostemma parviflorum*.—75, 76. *Gomphostemma wallichii*. Scales = 0.5 μm (63, 66); 1 μm (65, 68, 70, 72, 74, 76); 5 μm (62, 64, 67, 69, 71, 73, 75).



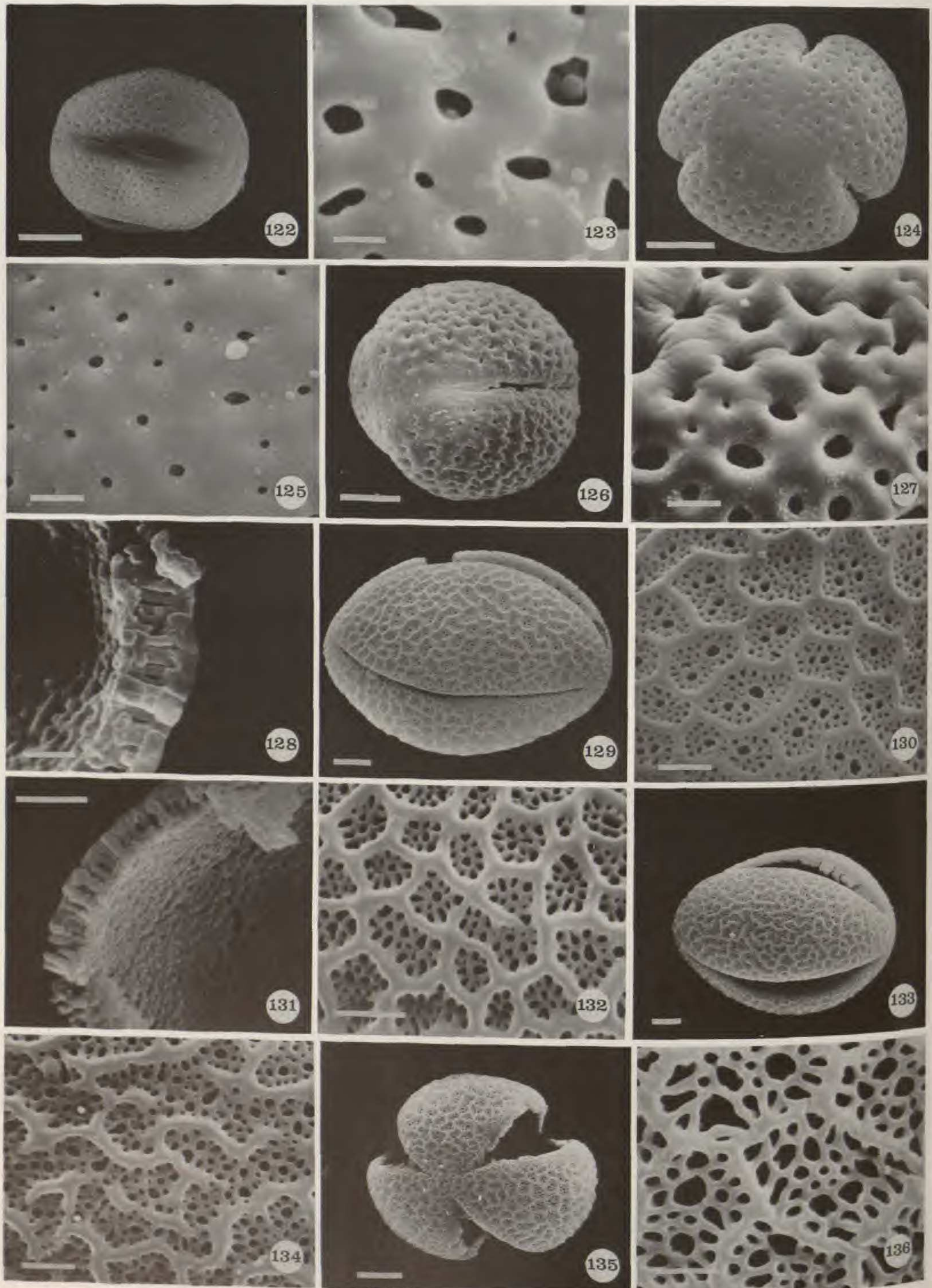
FIGURES 77–91. Pollen of Lamioideae: *Lagopsis*, *Lamiophlomis*, and *Lamium*.—77. *Lagopsis marrubiastrum*.—78, 79. *Lamiophlomis rotata*.—80, 81. *Lamium album*.—82, 83. *Lamium flexuosum*.—84, 85. *Lamium garganicum*.—86, 87. *Lamium galeobdolon*.—88, 89. *Lamium moschatum*.—90, 91. *Lamium purpureum*. Scales = 0.5 μm (83, 89); 1 μm (79, 81, 82, 84, 85, 87, 91); 5 μm (77, 78, 80, 86, 88, 90).



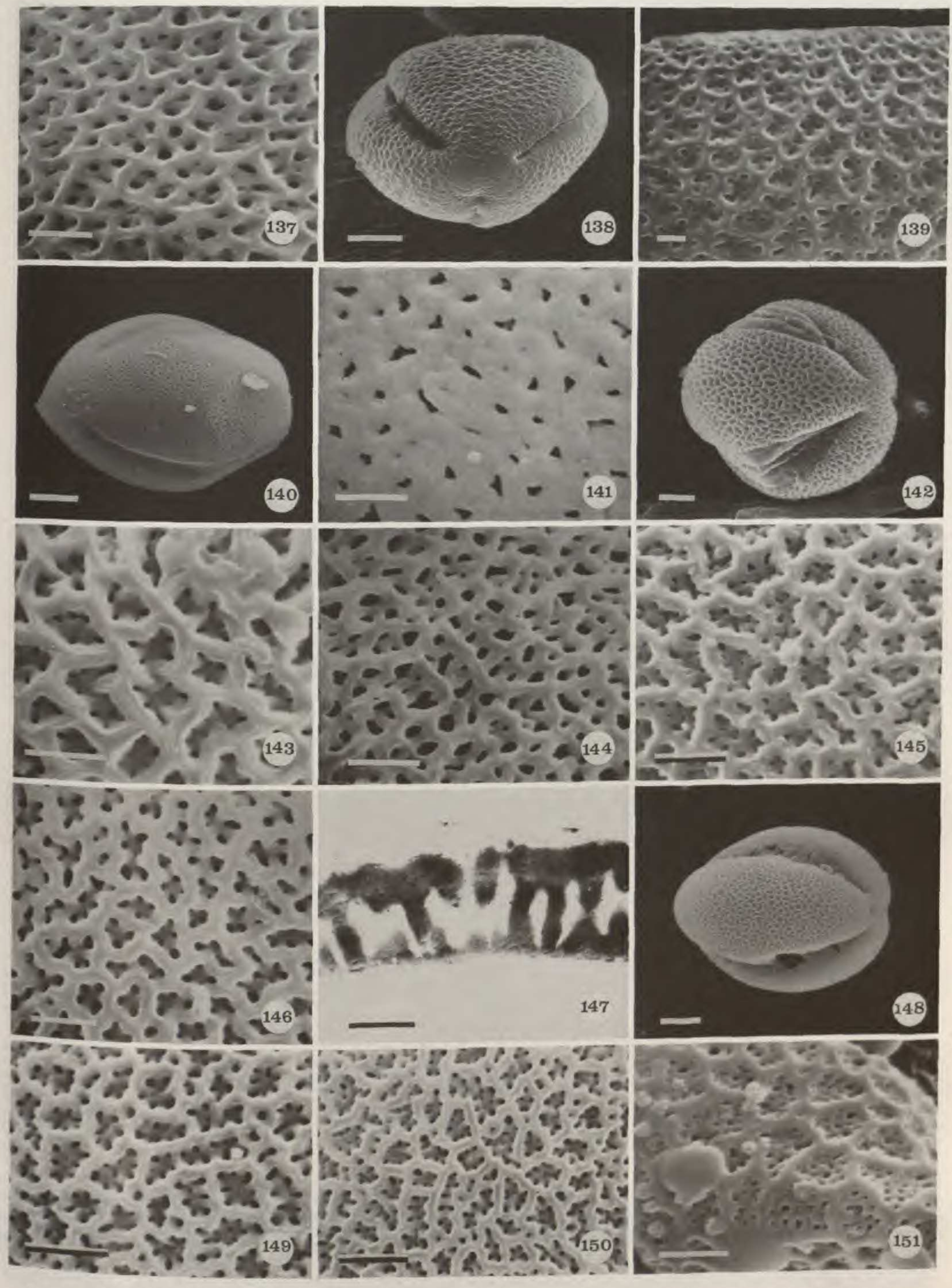
FIGURES 92–106. Pollen of Lamioideae: *Leonotis*, *Leonurus*, *Loxocalyx*, and *Macbridea*. —92, 93. *Leonotis bequaertii*. —94–96. *Leonotis leonitis*. —97. *Leonotis mollissima*. —98, 99. *Leonurus cardiaca* (*Swanson 811*). —100. *Leonurus sibiricus*. —101. *Loxocalyx ambiguus*. —102, 103. *Loxocalyx urticifolius*. —104. *Macbridea alba* (*Anonymous 4199*). —105, 106. *Macbridea caroliniana*. Scales = 1 μm (93, 95, 96, 97, 99, 100, 101, 103, 104, 106); 2.5 μm (98, 102); 5 μm (92, 94, 105).



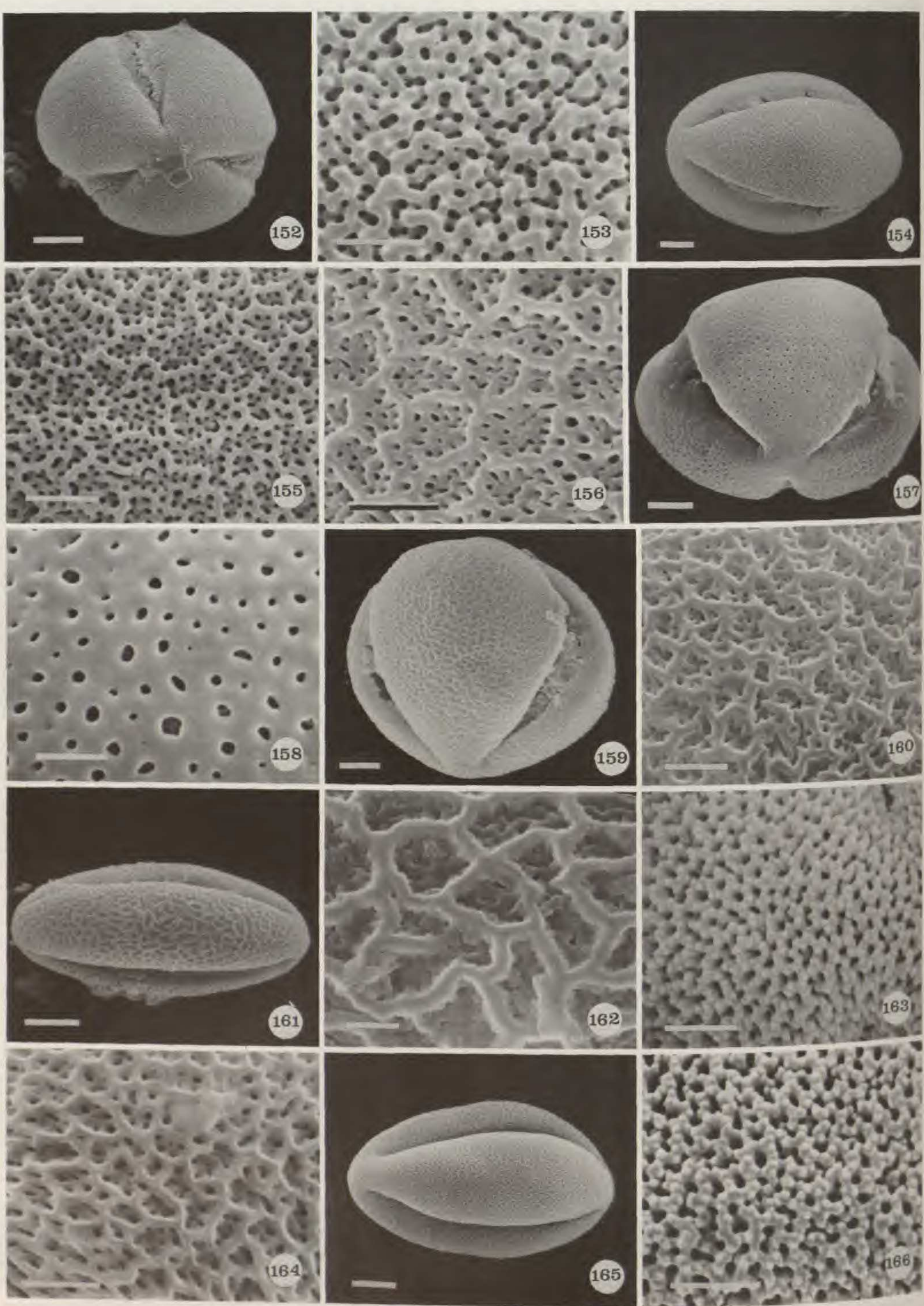
FIGURES 107–121. Pollen of Lamioideae: *Leucas*, *Melittis*, and *Metastachydium*.—107, 108. *Leucas abyssinica*.—109. *Leucas alluaudii*.—110, 111. *Leucas aspera*.—112, 113. *Leucas calostachys*.—114. *Leucas eriostoma*.—115. *Leucas hirta*.—116. *Leucas inflata*.—117. *Leucas javanica*—118. *Leucas rosmarinifolia*.—119, 120. *Melittis melissophyllum*.—121. *Metastachydium sagittatum*. Scales = 0.5 μm (117, 118); 1 μm (108, 109, 111, 113, 114, 115, 120); 2.5 μm (107, 110, 112, 116, 121); 5 μm (119).



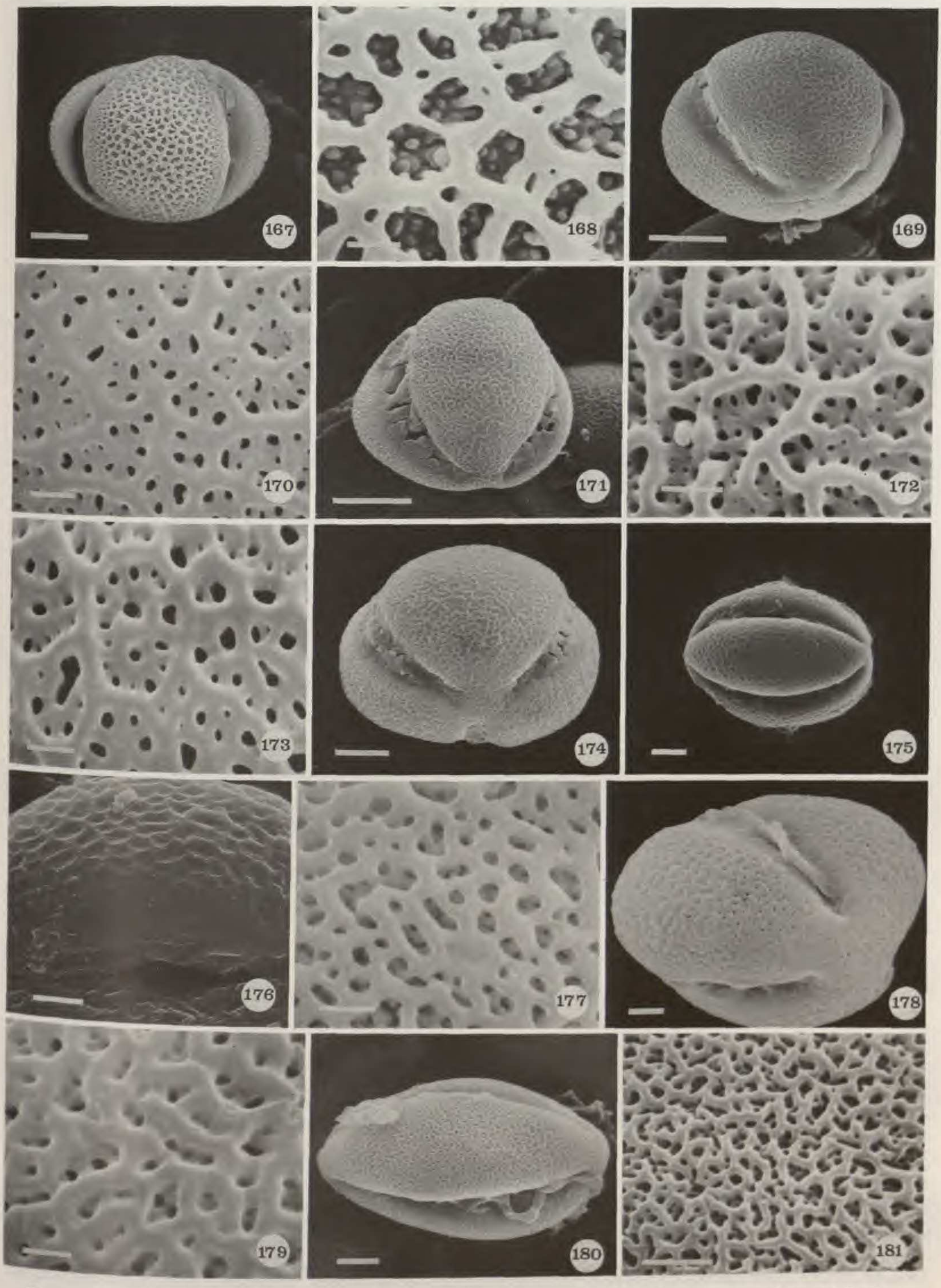
FIGURES 122–136. Pollen of Lamioideae: *Marrubium* and *Microtoena*.—122, 123. *Marrubium anisodon*.—124, 125. *Marrubium heterodon*.—126–128. *Marrubium supinum*.—129–131. *Microtoena delavayi*.—132. *Microtoena insuavis*.—133, 134. *Microtoena robusta*.—135, 136. *Microtoena urticifolia*. Scales = 0.5 μm (123); 1 μm (125, 127, 128, 130, 131, 132, 134, 136); 2.5 μm (129, 133); 5 μm (122, 124, 126, 135).



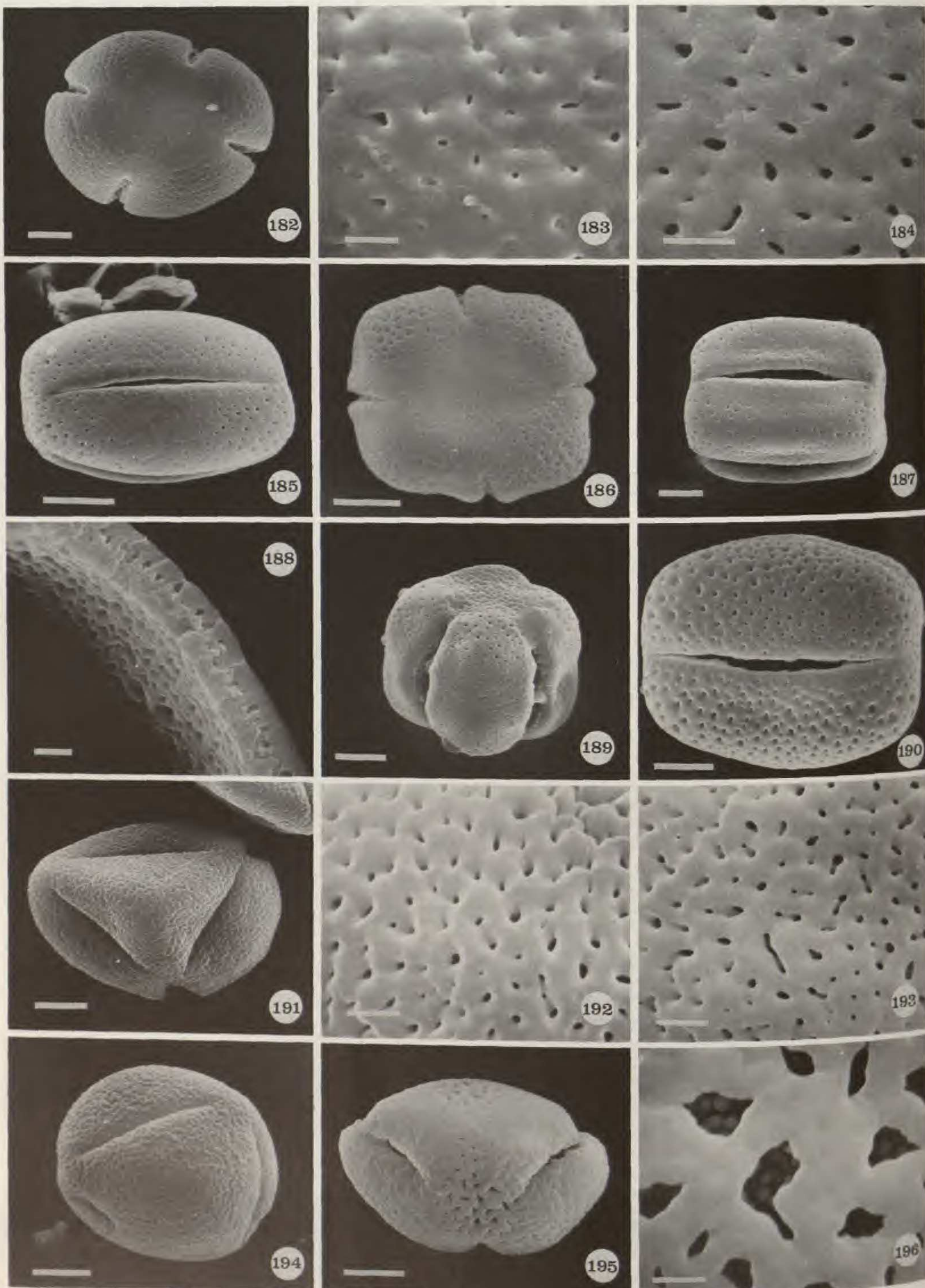
FIGURES 137–151. Pollen of Lamioideae: *Moluccella, Notochaete, Otostegia, Panzerina,* and *Paralamium.*—137. *Moluccella laevis.*—138, 139. *Moluccella spinosa.*—140, 141. *Notochaete hamosa.*—142, 143. *Otostegia fruticosa.*—144. *Otostegia integrifolia.*—145. *Otostegia repanda.*—146, 147. *Otostegia tomentosa.*—148, 149. *Panzerina lanata* (*Reverdatto 3775b*).—150. *Panzerina lanata* (*Steinberg & Prochorova 3459*).—151. *Paralamium gracile.* Scales = 0.5 μm (147); 1 μm (137, 139, 141, 143, 144, 145, 146, 149, 150, 151); 2.5 μm (142, 148); 5 μm (138, 140).



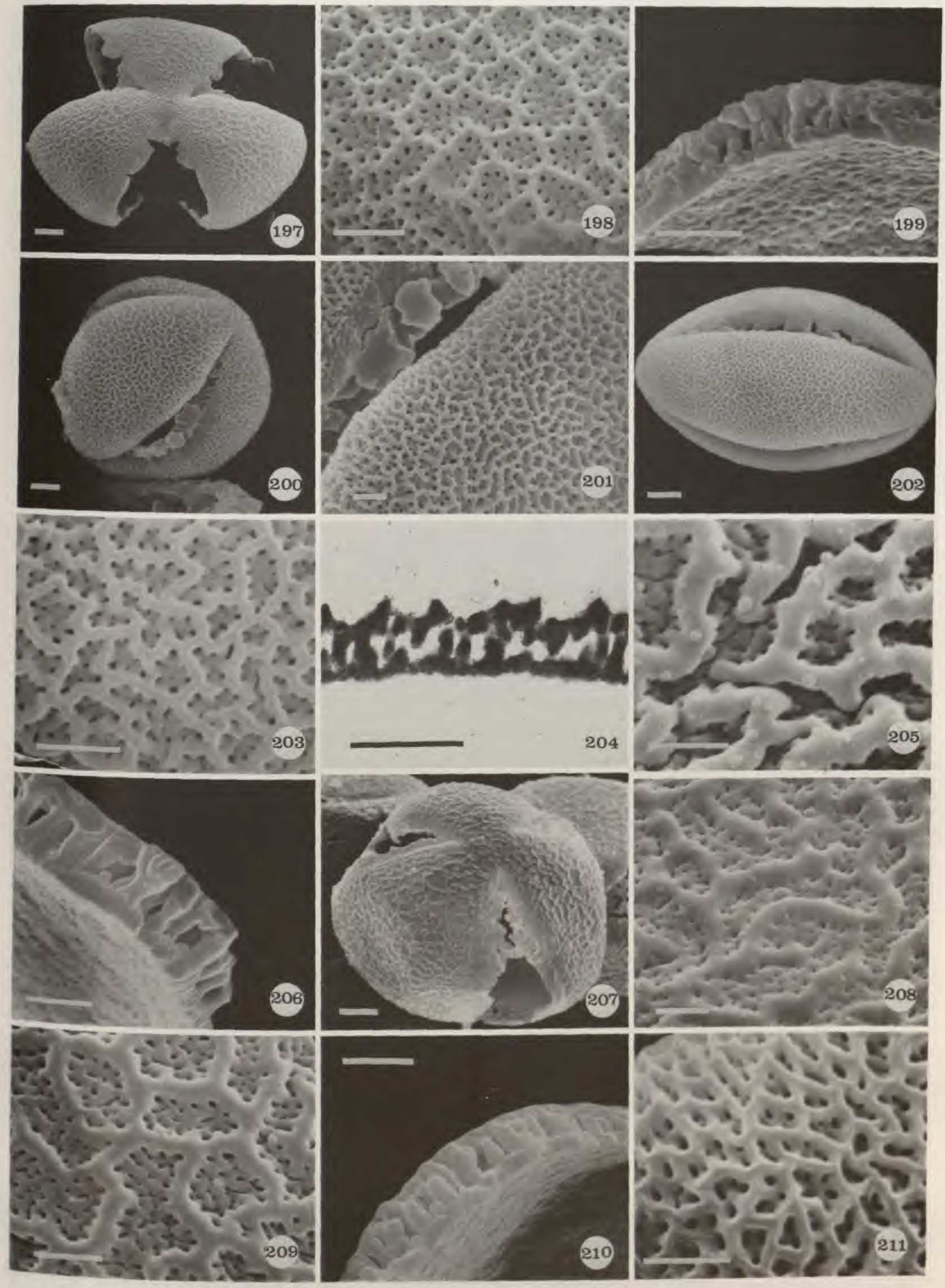
FIGURES 152-166. Pollen of Lamioideae: *Paraphlomis, Phlomidoschema,* and *Phlomis.*—152, 153. *Paraphlomis javanica.*—154, 155. *Paraphlomis lanceolata.*—156. *Paraphlomis rugosa.*—157, 158. *Phlomidoschema parviflorum.*—159, 160. *Phlomis agraria.*—161, 162. *Phlomis lanata.*—163. *Phlomis maximowiczii.*—164. *Phlomis tuberosa.*—165, 166. *Phlomis umbrosa.* Scales = 1 μm (153, 155, 156, 158, 160, 162, 163, 164, 166); 2.5 μm (154, 157, 159, 165); 5 μm (152, 161).



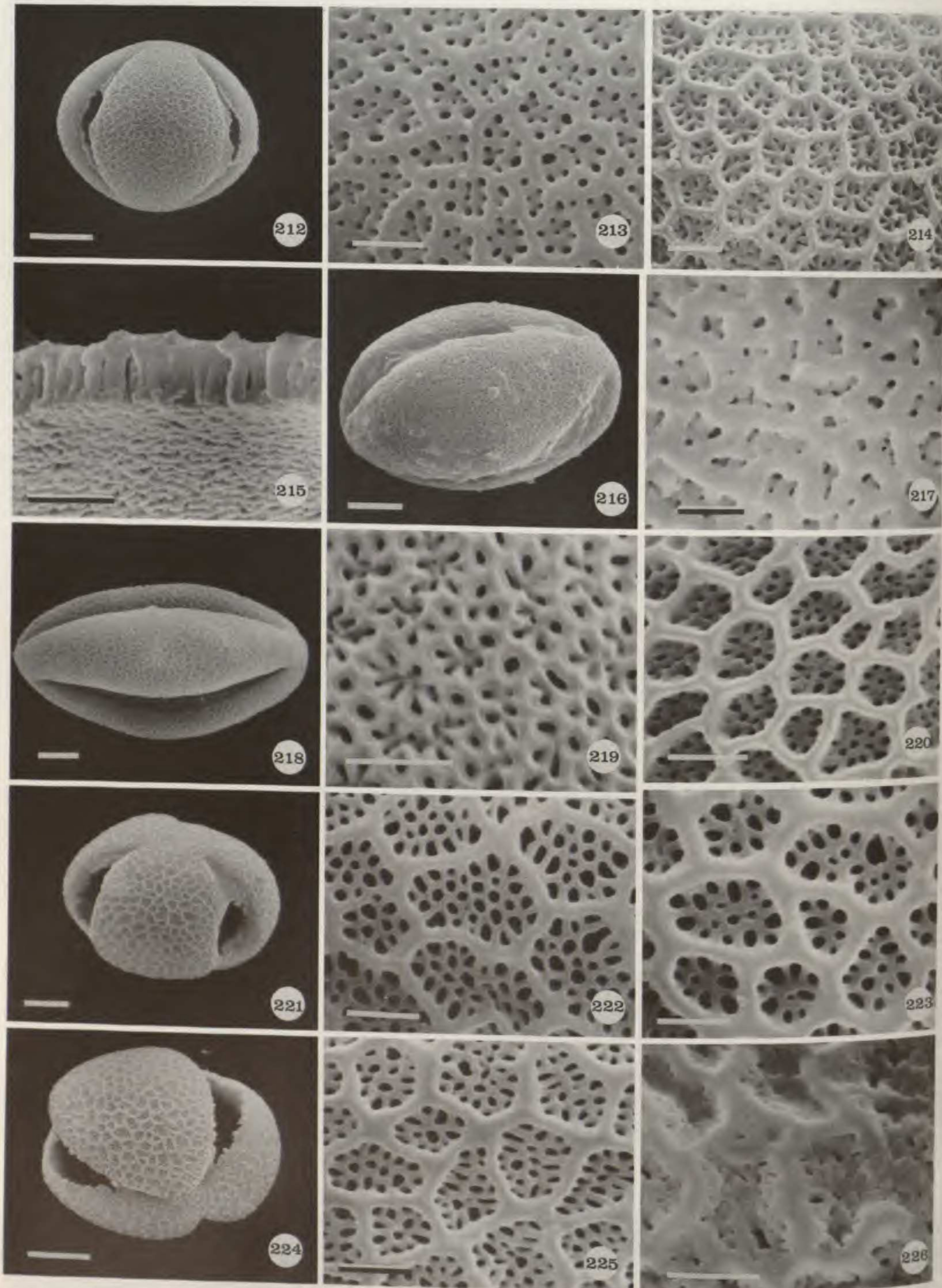
FIGURES 167–181. Pollen of Lamioideae: *Phyllostegia, Physostegia, Prasium, Pseuderemostachys,* and *Roylea.*—167, 168. *Phyllostegia grandiflora.*—169, 170. *Phyllostegia hirsuta.*—171, 172. *Phyllostegia hispida.*—173. *Phyllostegia lantanoides.*—174. *Phyllostegia racemosa.*—175, 176. *Physostegia longisepala.*—177. *Prasium majus.*—178, 179. *Pseuderemostachys sewertzowii.*—180, 181. *Roylea cinerea.* Scales = 1 μm (168, 170, 172, 173, 177, 179, 181); 2.5 μm (178, 180); 5 μm (174, 176); 10 μm (167, 169, 171, 175).



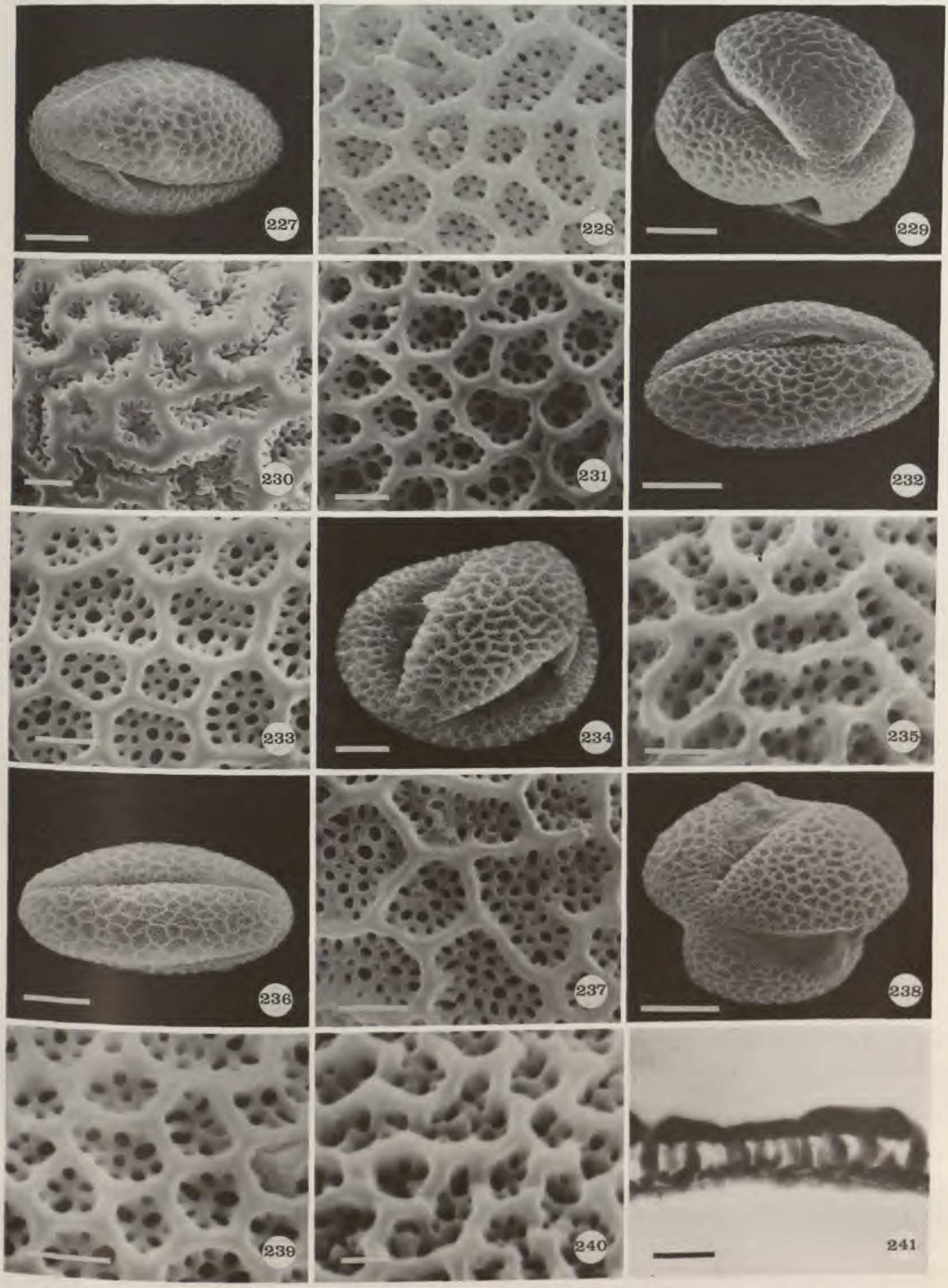
FIGURES 182–196. Pollen of Lamioideae: *Sideritis.*—182, 183. *Sideritis canariensis.*—184. *Sideritis candicans.*—185. *Sideritis curvidens.*—186. *Sideritis hyssopifolia.*—187. *Sideritis ilicifolia.*—188. *Sideritis lagascana.*—189. *Sideritis romana.*—190. *Sideritis villosa.*—191, 192. *Sideritis chlorostegia.*—193. *Sideritis euboea.*—194. *Sideritis hololeuca.*—195, 196. *Sideritis montana.* Scales = 1 μm (183, 184, 188, 192, 193, 196); 5 μm (182, 185, 186, 187, 189, 190, 191, 194, 195).



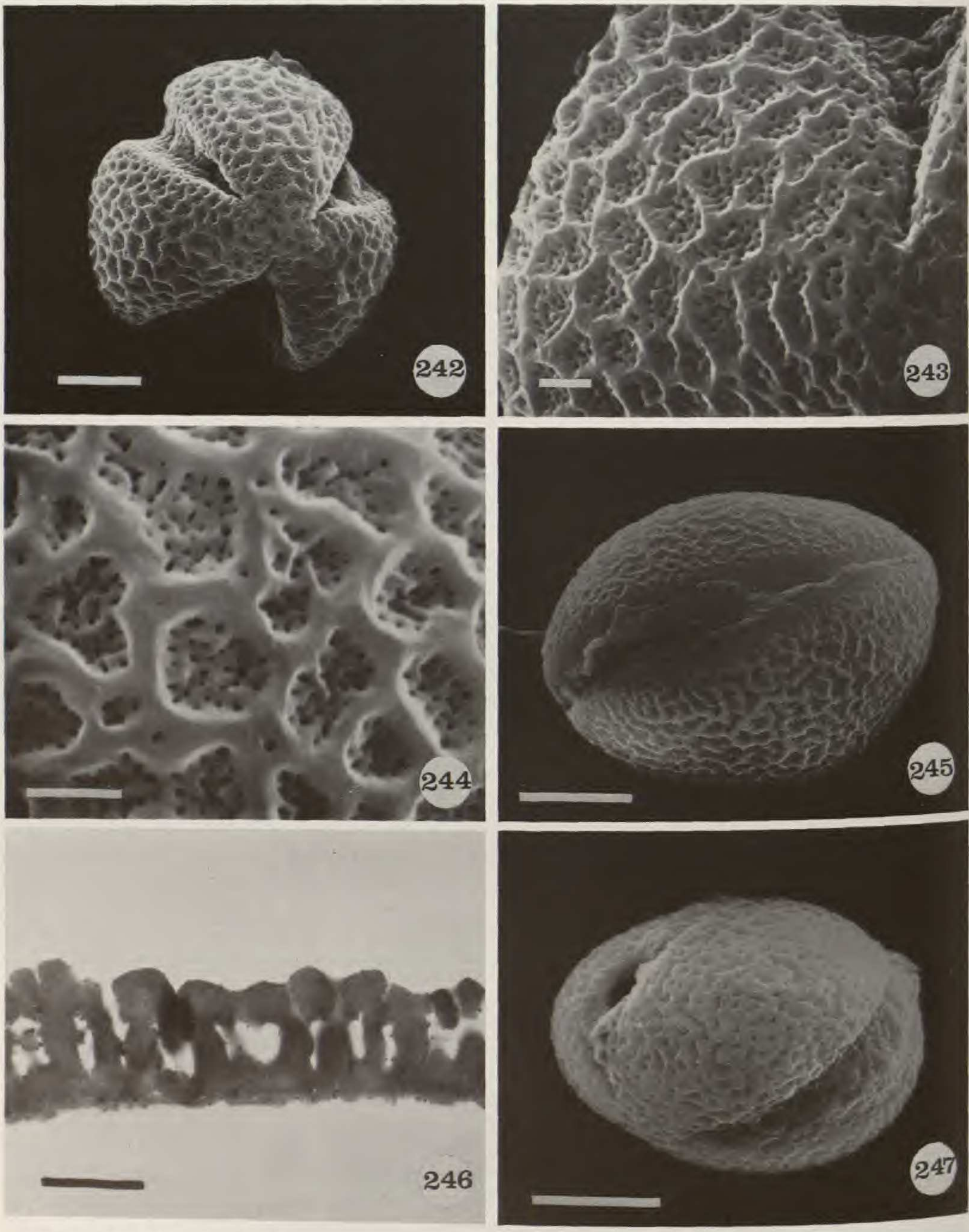
FIGURES 197–211. Pollen of Lamioideae: *Stachyopsis*, *Stachys*, *Stenogyne*, and *Sulaimania*.—197–199. *Stachyopsis oblongata*.—200, 201. *Stachys riddellii* (*Cantino 1229*).—202–204. *Stachys sylvatica*.—205, 206. *Stenogyne haliakalae*.—207, 208. *Stenogyne kamehamehae*.—209, 210. *Stenogyne purpurea*.—211. *Sulaimania otostegioides*. Scales = 1 μm (198, 199, 201, 203, 204, 205, 206, 208, 209, 210, 211); 2.5 μm (197, 200, 202); 5 μm (207).



FIGURES 212–226. Pollen of Lamioideae (*Suzukia, Synandra, Thuspeinanta, Wiedemannia*) and genera of uncertain affinities (*Anisomeles, Eurysolen*).—212, 213. *Suzukia luchuensis.*—214, 215. *Synandra hispidula* (*Hammer 6*).—216, 217. *Thuspeinanta persica.*—218, 219. *Wiedemannia orientalis* (*Kuntay 48*).—220. *Anisomeles heyneana.*—221, 222. *Anisomeles indica* (*Chun & Tso 43882*).—223. *Anisomeles malabarica.*—224, 225. *Anisomeles salviifolia.*—226. *Eurysolen gracilis.* Scales = 1 μm (213, 214, 215, 217, 219, 220, 222, 223, 225, 226); 2.5 μm (218); 5 μm (212, 216, 221, 224).



FIGURES 227–241. Pollen of Pogostemonoideae: *Pogostemon* and *Colebrookea*.—227, 228. *Pogostemon brachystachyus*.—229, 230. *Pogostemon cablin*.—231. *Pogostemon cruciatus*.—232, 233. *Pogostemon glaber*.—234, 235. *Pogostemon myosuroides*.—236, 237. *Pogostemon plectranthoides*.—238, 239. *Pogostemon yatabeanus*.—240, 241. *Colebrookea oppositifolia*. Scales = 0.5 μm (240, 241); 1 μm (228, 230, 231, 233, 235, 237, 239); 2.5 μm (234); 5 μm (227, 229, 232, 236, 238).



FIGURES 242–247. Pollen of Pogostemonoideae: *Comanthosphace*, *Leucosceptrum*, and *Rostrinucula*.—242, 243. *Comanthosphace japonica* (*anonymous*).—244. *Comanthosphace japonica* (*Ohashi & Murata s.n.*).—245, 246. *Leucosceptrum canum* (*Rock 6650*).—247. *Rostrinucula dependens*. Scales = 0.5 μm (246); 1 μm (243, 244); 5 μm (242, 245, 247).